

THE
ORIGIN OF BIRDS

GERHARD
HEILMANN

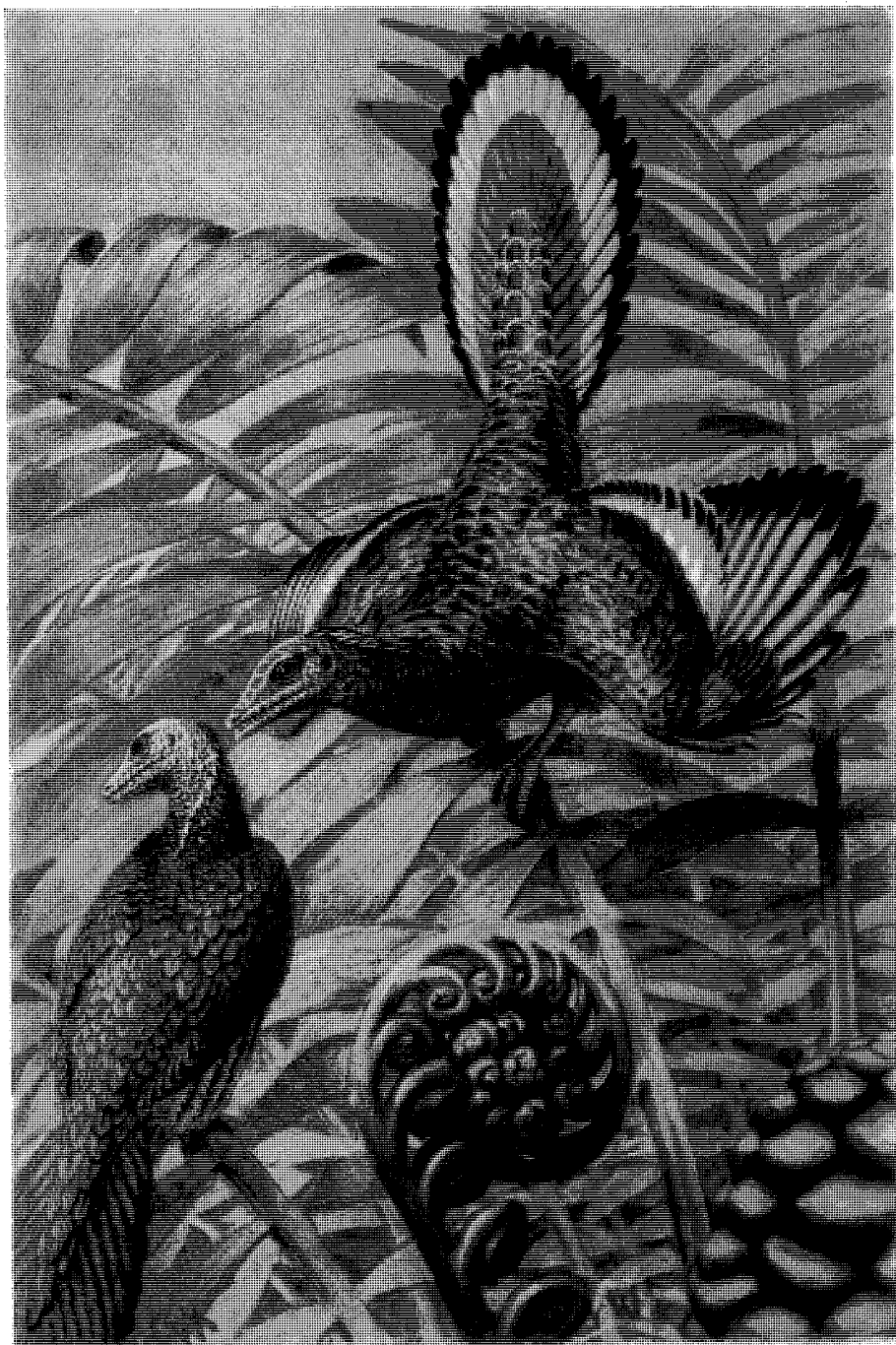
THE ORIGIN OF BIRDS - G. HEILMANN

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WITH

THE ORIGIN OF BIRDS

EGMONT H. PETERSEN
PRINTER TO THE ROYAL COURT
COPENHAGEN



Birds, from the Upper Jurassic (*Archaeornis*), male courting female. Painting by the author.

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BY

GERHARD HEILMANN

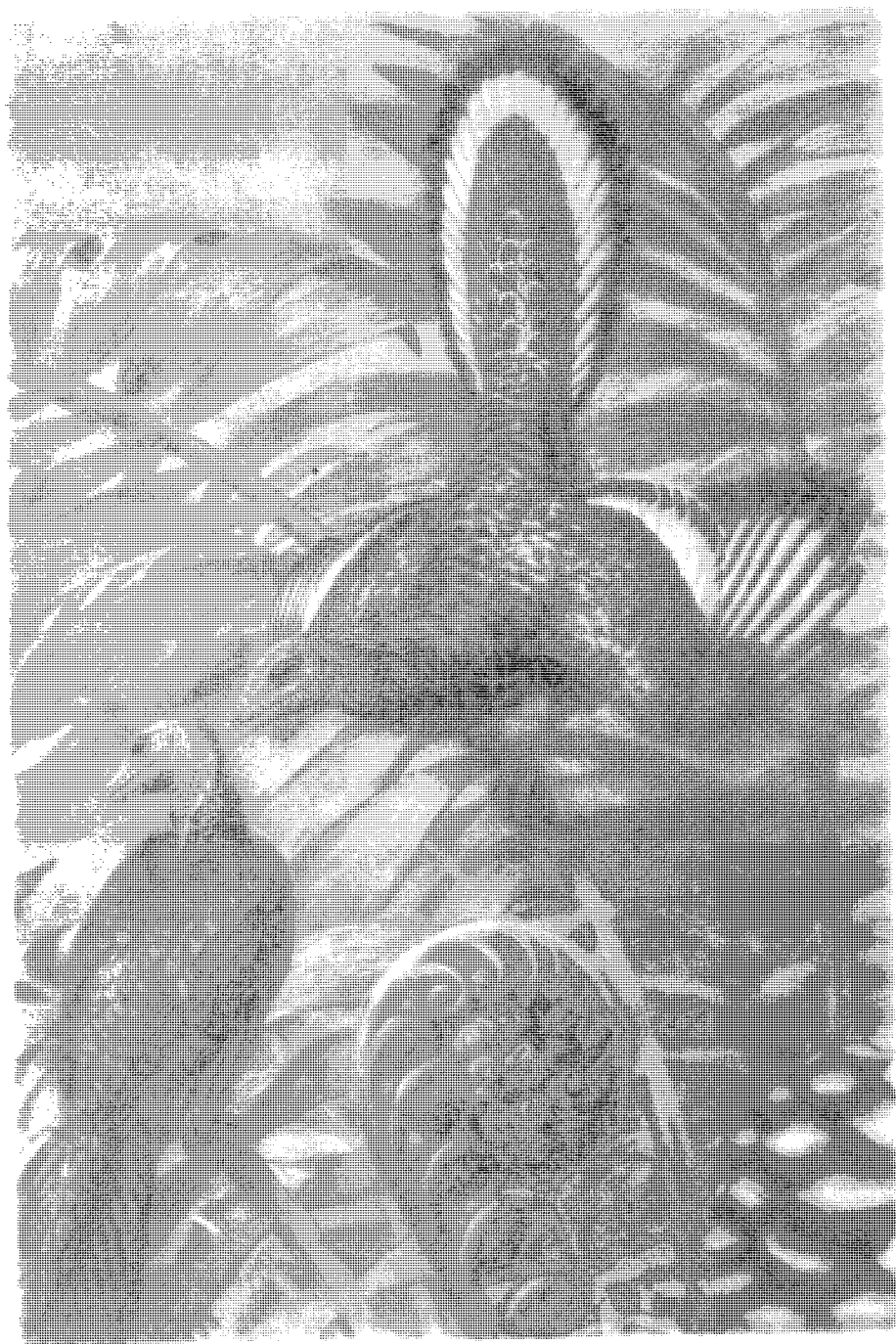
WITH TWO PLATES IN COLOUR
AND ONE HUNDRED AND FORTY
PHOTOGRAPHS AND TEXT FIGURES
FROM DRAWINGS BY THE AUTHOR

LONDON

H. F. & G. WITHERBY

326 HIGH HOLBORN, W.C.

1926



Using the *Diaper Jumpsuits* by *Infantino* as an example, a listing would look like this:

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PRINTED IN COPENHAGEN FOR
MESSRS H. F. & G. WITHERBY

PREFACE

Every phase of the evolution of animal life on our globe being of the utmost interest to every true lover of nature, I have in this book attempted to give an account of our present knowledge of the origin of birds, because the evidences now at our disposal are so manifold and conclusive that only a few minor particulars are still dubious.

The book makes an appeal to the scientist as well as to the lay ornithologist; hence, many facts well known to the former, will be requisite to the latter. I cannot, however, hope to make this section of the phylogenetic history intelligible to the layman without presupposing some knowledge and close attention on the part of the reader.

Although anatomy, especially osteology, may seem a rather tedious and forbidding study to most people, it will be necessary for the reader to acquaint himself with some parts of same, in order fully to understand the following pages. And when the first dislike is overcome, the form and the specialization of the bones will by no means be found less interesting than for instance the exterior of the bird.

On closer inspection, the skeleton proves to be something more than a firm timber work, supporting the whole organism; in spite of its hard and solid structure, it is of a marvellously plastic material, so much so that every tiny ridge or groove betrays its special use, informing us most implicitly of the forces that have been at work in its formation.

For the study of the individual bones of the skull I particularly wish to call the lay reader's attention to fig. 3, and for an illustration of the whole skeleton of birds, to fig. 23.

From the very outset it was clear to me that for this small section of the phylogenetic evolution, in order to be as intelligible as possible, perspicuity was to be aimed at. To this end I endeavoured, during the preparation, to garb the scientific facts in an artistic form, attempting not in drawings only, but also in words, to impress images upon the mind of the reader.

As a matter of fact, pictures are more easily apprehended and remembered; their influence is also deeper and more permanent. The abstract truth-seeking of science may in many cases need, for a complement, the more tangible elucidation of art. And art possesses something spontaneous, too, something auspicious, a sort of sixth sense, which in its very nature is exotic to science. It gives expression to something of the deepest in human nature, and dimly responds to its sense of harmony with the remote past during the rise and evolution of life on our globe. A union of art and science I should consider the highest attainable ideal, and paleontology, in particular, would furnish but a meager and deficient image of the past without the aid of art.

In order to make the skeletal structures as well as the exterior of extinct animals appear as correct as possible, and in their true proportions, when drawn in perspective view, I have modelled these in a plastic material (plasticine). From such models are drawn for instance the reconstructions of the skulls of Archaeornis and Hesperornis, and the pelvis of Archaeopteryx. An illustration as that of the three Gorgosaurs at the carcass of a Stegosaur (fig. 123) would have been impossible for me to draw in the correct proportions without such models. So I modelled all four animals, posed them in the desired group, and threw a strong electric side-light upon them. Then, of course, it was an easy task to make a drawing of this idyl from the Cretaceous. In fig. 132 the desert-plants, too, are modelled beforehand.

I am under great obligations for much valuable assistance from Dr. R. W. Shufeldt of Washington, who has taken the pains of furnishing photographs of rare specimens, specially for this work (figs. 47, 2; 48; 83 and 84). Also to Professor R. S. Lull of the Yale University I am much indebted for amiable help and for permission to reproduce a photograph of the pubis of Podokesaurus (fig. 121). Professor Lull has further sent me some photographs of details of the Hesperornis-skull, and it was mainly at his kind instigation that I started afresh upon this edition of the origin of birds.

In September 1923 I was in Berlin to study Archaeornis at the Museum für Naturkunde, and was there received with the greatest courtesy and kindness by Professor J. F. Pompeckj, who placed the unique fossil at my disposal, in a room with excellent light, thus enabling me to study and draw every detail of this Jurassic bird under the most favourable conditions.

The British Museum of Natural History has rendered me very valuable aid, not only in furnishing me with an excellent photograph of Archaeopteryx (fig. 1), but also by forwarding a coloured plaster-cast of the pelvic region of the fossil. Without the latter it would have been impossible to illustrate the pelvis of Archaeopteryx so fully as has been done in figs. 9, 12, and 13. Also to Dr. A. Smith Woodward and Dr. I. A. Bather of the Geological Department I am greatly indebted for very valuable information.

To all these gentlemen I hereby render my most sincere thanks.

It is in Denmark a difficult and thankless task to study Paleontology. At our university, neither Paleozoology nor Paleontology is taught, not to speak of Paleobiology. Hence, it is no wonder that, even amongst highly cultivated men, dense ignorance as to the importance of these subjects prevails; their very names are hardly known. Anything like the very great benevolence and good-will which I have met with from several foreign scientists, I am sorry not to be able to record of my own countrymen.

Copenhagen, June 1925.

GERHARD HEILMANN.

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PART I

SOME FOSSIL BIRDS

INTRODUCTION

WITHIN the animal kingdom there are hardly two classes which, at a glance, differ more from one another than the reptiles and the birds. Take, for instance, a nightingale and a tortoise, or the secretary bird warding off the poisonous bite of the African cobra: there seems to be no similarity between them but this that both of them are vertebrate animals.

Every move of the bird is characterized by its warm pulsating blood; its passions are strong, and its feeling so intense as to vent itself in song. Its gait is upright, powerful wings lift it without apparent effort into the highest regions of the air, and thence it is able to descend to the earth with the utmost speed, protected by its warm plumage from the greatest variations in temperature, while its vision may be adjusted immediately to any distance, thus enabling it, with equal ease, to sight its quarry from afar or near.

The reptile seems to be the very opposite to all this. Sluggish and slow it creeps along; it takes sunshine and heat to stimulate it to action; the cold paralyzes its every movement. The body is covered with scales, or is mailed, and its four limbs are all used in its progress along the ground. The forelimb has no resemblance to the bird's wing, and the jaws are usually toothed.

All these, however, are only superficial differences. The outward appearance disguises, as it were, the amazing and profound conformity subsisting between the two classes, to which in the following pages we shall call attention. We must also bear in mind that birds and reptiles of the present day are the final descendents of two different lines in the evolutionary process, diverging widely from each other through an immense space of time.

In order to understand this, we must first of all study the birds which lived in the remote past, millions of years ago.

If we take into account what little remains of the many thousands of animals which are dying every day, for the most part vanishing in the bellies of their fellows, we are the better prepared to appreciate that unusually favourable conditions are required for the remains of an animal to be preserved through countless ages; for this is possible only if the body, immediately after death, is covered by a layer of sand or the like, so that it is completely protected from the influences of the atmosphere and other destructive agencies.

The remains of such animals from past ages, which are buried in the earth, are termed fossils. Generally teeth and bones only are preserved, and these have undergone a process of mineralization termed petrification. In exceptional cases, however, skin, muscular tissue, and intestines are also preserved, and

thus we are able to study, in certain cases, not only the external form, but also the inner structure, usually by cutting it into thin microsections.

As a result of volcanic eruptions, mountain-slides, spring-tides, inundations, sand-storms, and similar disturbances, many animals are overwhelmed and immediately buried in sand or some other material which preserves them from the ravages of decay. Others plunge into mire or bogs, or end their lives in their caves. Protracted periods of drought also give rise to the death of many animals.

The flying birds have better chances of escaping all these perils, and hence their remains are very rare amongst fossils; but in return they furnish the most remarkable and important material for our study of the origin and the evolution of their class.

The past history of the earth is divided into different periods. The oldest in which animal remains are to be found, is named the Cambrian period; then follow in order the Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, Tertiary, and Quarternary periods; the last includes the era in which we now live. The Tertiary period is subdivided into the Eocene, Oligocene, Miocene, Pliocene, and Pleistocene eras.

ARCHAEORNIS AND ARCHAEOPTERYX

The lithographic quarries of Bavaria, whose deposits belong to the Upper Jurassic era, have become famous for their great number of well preserved fossils. In this lithographic quarry at Solenhofen the remains of a bird-like being was found in the year 1861, unfortunately in a rather defective condition. This unique fossil was bought by the authorities of the British Museum and described by Richard Owen (1) as the remains of a bird, *Archaeopteryx lithographica* (fig. 1).

On the left of this limestone slab, we see the complete left hind-limb. Right opposite is the other hind-limb, of which but the femur and tibia are preserved; the foot is wanting. Between them lies its singular tail, nearly complete, with all its rectrices in position on the twenty slender tail-vertebræ. Just above the tail are the two pubes united in a symphysis; between them is the ischium. On the top of this are the acetabulum and the ilium, thus making the right side of the pelvis complete. Close to the pelvis is the right scapula in dorsal view; at the end of this is seen the upper end of the right coracoid. The black spot is a hole in the slab, made in order to uncover the front of the bone. Joined to this is the right humerus in ventral view. Its distal end is obscured, and so are the proximal parts of the right ulna and radius lying beside it. In front of the distal ends of these two bones a carpal element is seen. On the other side are the left humerus, ulna, and radius, and above them some metacarpals and phalanges of the hand. In the middle there is a curved bone interpreted as the furcula. Some impressions of remiges are also discernible.

Fortunately, a second Jurassic bird, in a much better state of preservation,

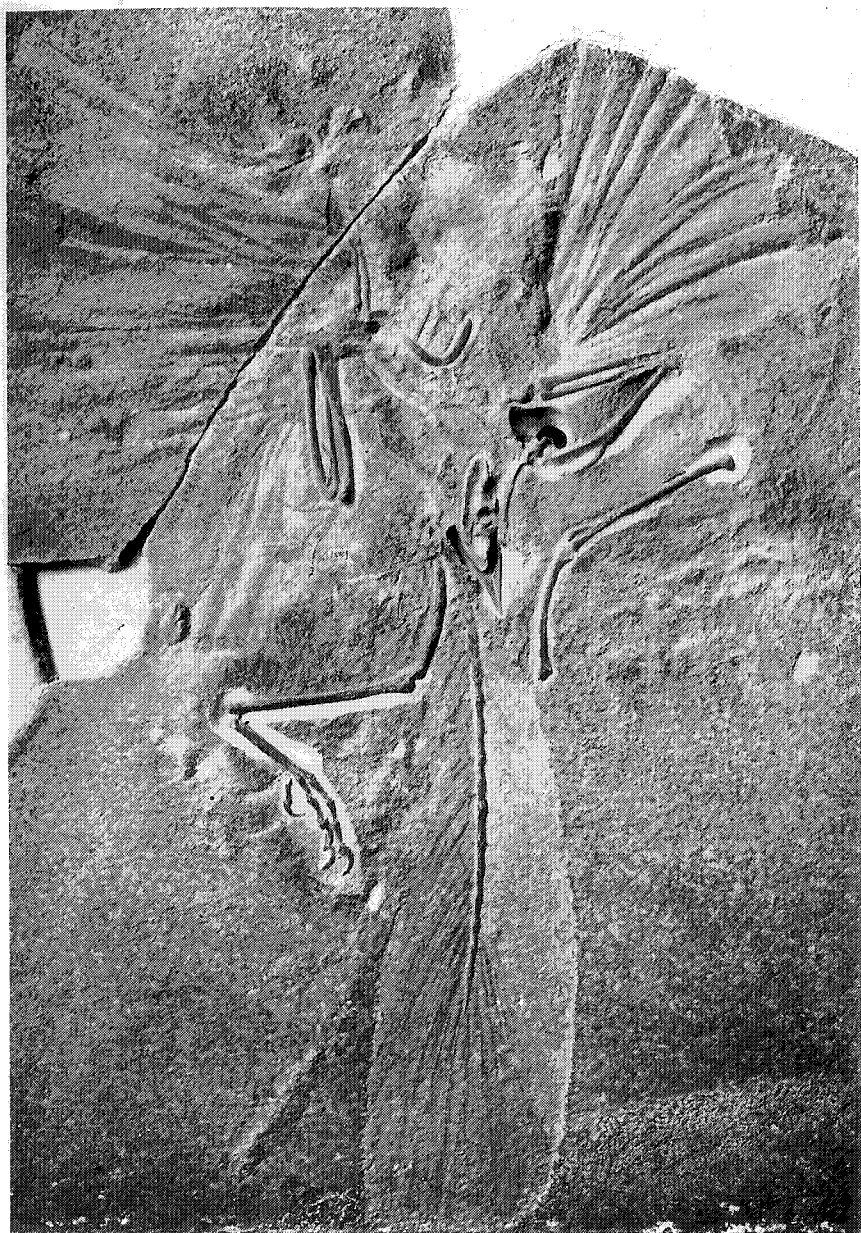


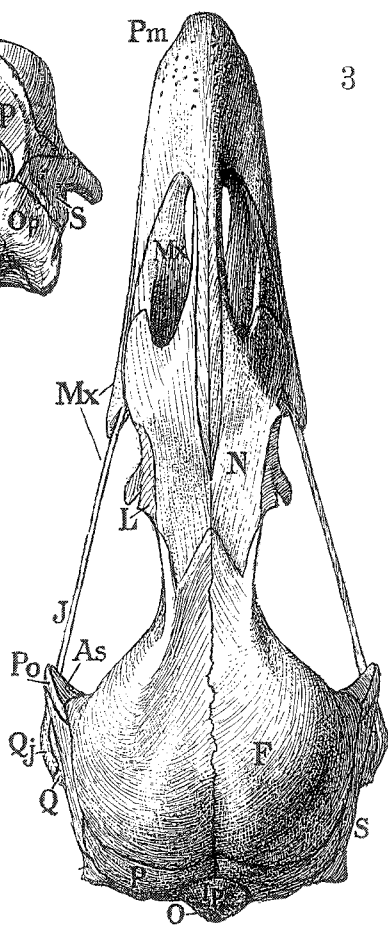
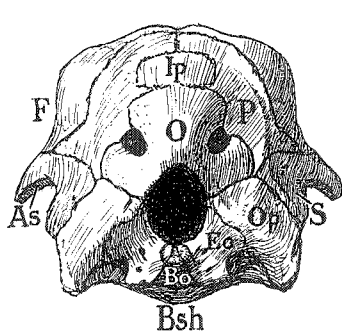
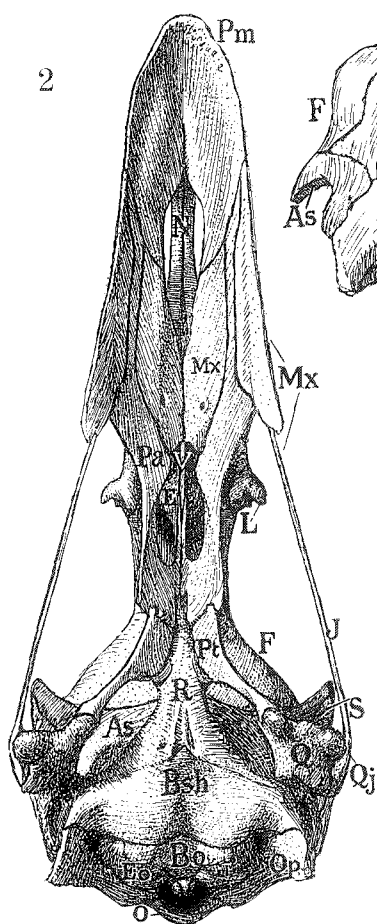
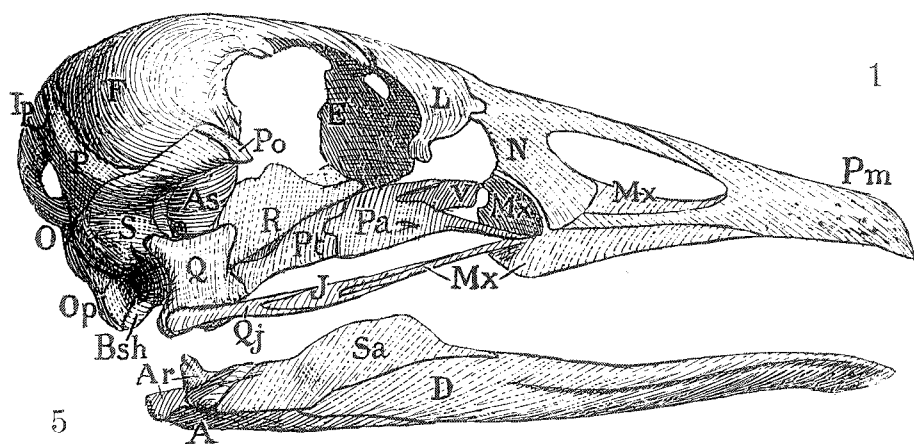
Fig. 1. *Archaeopteryx lithographica* Owen, from a photograph of the original in London, reproduced by special permission of the Trustees of the British Museum; $\frac{1}{13}$ nat. size.



Fig. 2. *Archaeornis siemensi* Dames, from a drawing in nat. size, made



...author directly from the fossil in Berlin. The reproduction is $\frac{1}{2}$ nat. size



was found in 1877 near Eichstätt, Bavaria. This is now in the Museum für Naturkunde in Berlin, and was described by Dames (2).

Fig. 2 shows this remarkable specimen with out-stretched wings, displaying all its strange features on the limestone slab. With a generous hand Nature has here stretched out this most interesting skeleton to our view, so as to make nearly all the details fully distinguishable.

This fossil, well preserved as it is, presents an unusually fine spectacle. The smooth, bright bones, with their warm tawny hue, stand out boldly from the yellowish-grey limestone, which constitutes a natural foil. In some places the bones have a metallic tint, and the light reflects itself beautifully in the most prominent parts. Add to this the impression of feathers, more or less distinct, investing the whole thing with a singular beauty, and we cannot but feel, so to speak, the pulsations of life from an infinite past. We note the delicate barbs in the vanes of the remiges and rectrices, supported by the rigid feather-quills, and further the soft contour feathers, which, like a mass of light clouds, surround the body. Even a distinct toe-pad is preserved; it is discernible just under the distal articulation of the third toe of the left foot, the rough surface of the skin being traceable.

Some years ago the *Archaeopteryx* in the British Museum was further developed, and the two pubes and coracoid came to light (3). It has also been stated by Petronievics (4) that the Jurassic bird in Berlin belongs to another genus than the specimen in London, and therefore it has been given another name: *Archaeornis siemensi*.

The following description deals mainly with *Archaeornis*, which I have myself studied in Berlin; but in many details, such as the pelvis, the foot, and the coracoid, use has been made of papers on the London *Archaeopteryx* (3 and 4), and of photographs, and a plaster cast of this fossil, kindly forwarded by the British Museum authorities.

The skull of *Archaeornis*, is in a bad state of preservation, the thin and fragile bones being strongly compressed and partly crushed by the weight of layers of rock. It may also be that some of the more obscure details are due to imperfect preparation. Fortunately, crystals of calcite preserve the form of the bones in many places, and the small pieces of bone still adhering to them show the original extension of the entire bones.

In order to understand this interesting skull completely, it is necessary to be acquainted with the individual bones of a recent bird's skull, and this may best be done by studying quite young specimens, because later on the bones will rapidly coalesce, thus obscuring the sutures. As illustrations of birds' skulls in anatomical works and text-books are not only unsatisfactory,

Fig. 3. Skull of a wild gosling (*Anser ferus*), considerably enlarged, 1 lateral aspect, 2 palatal view, 3 upper view, 4 posterior view, 5 mandible. A angular, Ar articular, As alisphenoid, Bo basioccipital, Bsh basisphenoid, D dentary, E ethmoid, Eo exoccipital, F frontal, Ip interparietal, J jugal, L lachrymal, Mx maxillary, N nasal, O supraoccipital, Op opisthotic, P parietal, Pa palatine, Pm premaxillary, Po postorbital, Pt pterygoid, Q quadrate, Qj quadratojugal, R basisphenoidal rostrum, S squamosal, Sa surangular, V vomer.

but may also contain misleading errors (5), I have in fig. 3 drawn the skull of a wild gosling (*Anser ferus*) and enlarged it considerably, so as to demonstrate all the bones distinctly. A textual description is unnecessary here; any one may make himself familiar with the position and extension of the individual bones by studying the drawing. These will be mentioned many times in the following pages, and their names will not be repeated in the text to the illustrations, and so I beg the reader to learn them by heart now.

The hindmost part of the skull seems to be somewhat defective, but much more than what is now discernible, can scarcely have been present. The uppermost neck vertebræ are certainly not complete, but nevertheless they lie in their natural position. A little above the point where the uppermost one touches the skull, the foramen magnum was probably situated, directed straight backwards and not downwards.

In "Odontornithes" p. 120, Marsh states that the occipital condyle of *Ichthyornis* is directed backward, and that above the condyle the occipital portion of the skull is nearly vertical. This also seems to have been the case in *Archæornis*, and since the birds of the Cretaceous period prove to have small braincases and diminutive brains, there is no reason for supposing that the brain of *Archæornis* should have been large and well developed.

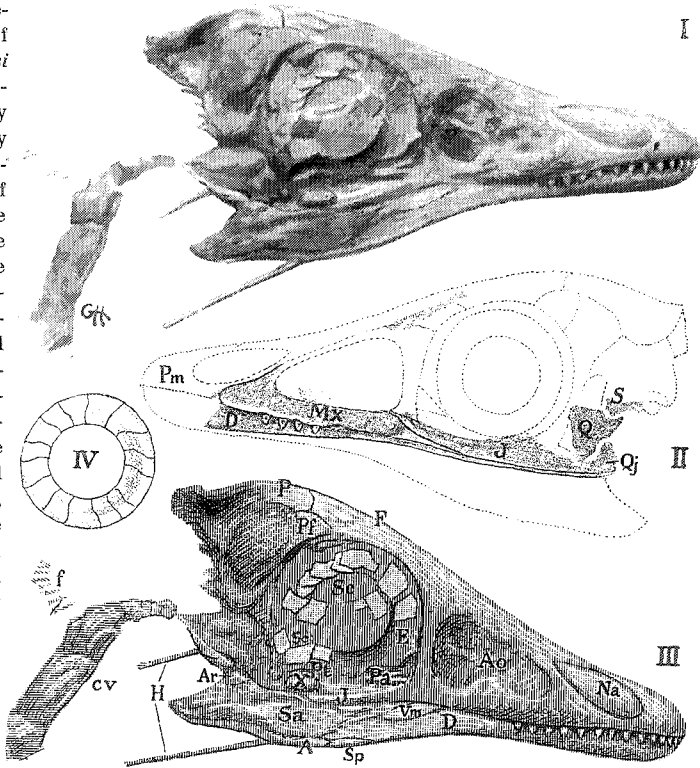
Using a strong magnifying-glass, I have drawn the skull directly from the fossil, twice its natural size, and this drawing is reproduced in fig. 4, I, somewhat reduced, and I have repeated it in fig. 4, III with letters added for explanation. Here the right side appears, but on the back of the stone a small part of the left side is uncovered, as seen in fig. 4, II, which also shows the outline of the skull restored.

There is a conspicuous depression where we might expect to find the supratemporal vacuity, but no definite hole is discernible. Possibly there was no supratemporal opening, but it may also be that there was a slit-like hole, and that this, owing to the strong compression of the skull, is now no longer visible.

A mould of the postfrontal (Pf) is discernible, and so is the suture between P and F, and between Pf and P and F. The impressions in the stone behind the orbit can scarcely be due to bones, but on the left side of the skull (fig. 4, II) this part is so well preserved that the quadrate, a piece of the squamosal, and the quadratojugal are visible.

Nearly the whole circumference of the very large orbit can be made out with certainty; only in the lower hindmost part is its form somewhat obscure, but here the left side of the skull furnishes us with the desired information, the upper margin of the jugal marking its inferior limit. In the middle we see the annular mould of the sclerotic, or outer coat of the eye, while the bony plates (Sc) of the sclerotic circle lie scattered around, some of them across the middle of the ring. Four of them, the highest on the left, seem but little displaced from their natural position, and we see how one overlaps the border of the next. In fig. 4, III, I have drawn these tiny plates without shading so as to make them more conspicuous. They are irregularly quadrangular as in recent birds, and 14 of them may

Fig. 4. I Right side-view of the skull of *Archaeornis siemensii* drawn $\frac{2}{3}$ nat. size directly from the fossil by the author and slightly reduced in the reproduction, II what is seen of the left side of the same skull, entered into the supposed outline, III the same as in I with lettering added, IV sclerotic ring of Red-breasted Merganser (*Mergus serrator*). Ao antorbital fenestra, H the two cornua of the hyoid bone (os hyoides), Na nasal opening, Pf postfrontal, Sc sclerotic plates in the orbit, Sp splenial, Vm vacuity in mandible, X indeterminate bone, cv cervical vertebrae, f impression of feathers.



be traced, more or less completely preserved.

The number in birds varies from 10 to 17; in fig. 4, IV, I have drawn the sclerotic ring of a Red-breasted Merganser (*Mergus serrator*), composed of 15 plates, and it shows how irregularly these are arranged, some overlapping their neighbours with both margins, while some are broad and others narrow. Such sclerotic plates occurred already in the Stegocephalians, and they are doubtless an inheritance from reptiles. Both in birds and reptiles these ossicles are similarly developed, and are not found in mammals. Seeley, in referring to the Pterosaurs ("Dragons of the air", p. 65), says that their "sclerotic circle of overlapping bones is formed like those in nocturnal birds"; but he furnishes no illustration. The ring is also preserved in Ichtyosaurs, Dromasaurs, Thalattosaurs, Mosasaurs, Geosaurs, Trachodonts, and Pseudosuchians.

A small deeply-recessed, somewhat rounded element marked X, at the bottom of the orbit, is so entirely without character that it is impossible to decide what it might have been: perhaps it was a part of the basisphenoidal rostrum or of the broad jugal, but it may not have anything to do with the skull at all. Above this lies what is probably the pterygoid, and a little further in front are the two bony edges of the palatine.

On the right side of the skull the posterior part of the jugal seems to be covered with the articular and surangular of the mandible, but on the back of the stone we see the jugal, very broad posteriorly, almost complete, and further the

characteristic suture between this and the toothed maxillary, greatly extending backwards, beneath the jugal, so that this last bone gets rather thin where it joins the adlachrymal, being wedged between Al and Mx. Likewise the foremost border of the maxillary is quite conspicuous. By a lucky chance the maxillary here shows the lower limit of the antorbital fenestra, for in the right profile the extent of this opening is somewhat obscured inferiorly.

The bony bridge separating the antorbital fenestra from the narial orifice is quite intact, but is very narrow and slender. The pre-orbital bridge, on the other hand, is broken, but by means of the remaining pieces its course may be followed with some degree of certainty. It is composed of the adlachrymal, which inferiorly has a broad connection with the jugal, so that no movement at this point was possible, the reverse of that in recent birds. Further, from the shape of the jugal posteriorly and from the relationship of the quadratojugal to the quadrate, it is evident that the mobility of the quadrate has been so small that the skull of *Archaeornis* may be termed akinetic. In this respect it may be contrasted to the mesokinetik skulls of recent birds, which as a rule have no adlachrymal, and whose pterygoid-palatine is capable of gliding along the sphenoidal rostrum, the forward movement of the quadrate being passed on to the jugal arch, in this way raising the upper beak.

The maxillary and premaxillary are provided with 13 teeth, all implanted in distinct sockets. They are nearly alike in size and form, and their distance apart is fairly even. Their crown is conical, somewhat narrowed at the base, and has (according to Dames) a sharp edge behind, from the apex downwards.

The almond-shaped narial aperture stands out clearly in its delicate frame of bone. The two large cornua of the hyoid bone are very conspicuous. My drawing shows what further details are distinguishable.

The lower jaw is amongst the most markedly defined parts of the skull, but the upper margin of the distal end passes beneath the maxillary, while the proximal end conceals the hindmost part of the jugal. The left side of the skull (fig 4, II) shows but very little of the mandible. The four bones, dentary, angular, surangular, and articular, ordinarily found in recent birds, are also found here, as also a vacuity between the dentary and surangular. However, a splenial seems to be visible too, and this is a reptilian feature, because in modern birds the splenial is to be seen only on the inside of the mandible, and does not extend round the inferior margin (see also fig. 32). The uppermost part of the dentary being concealed by the maxillary, no teeth, which we may safely presume to be present, are visible.

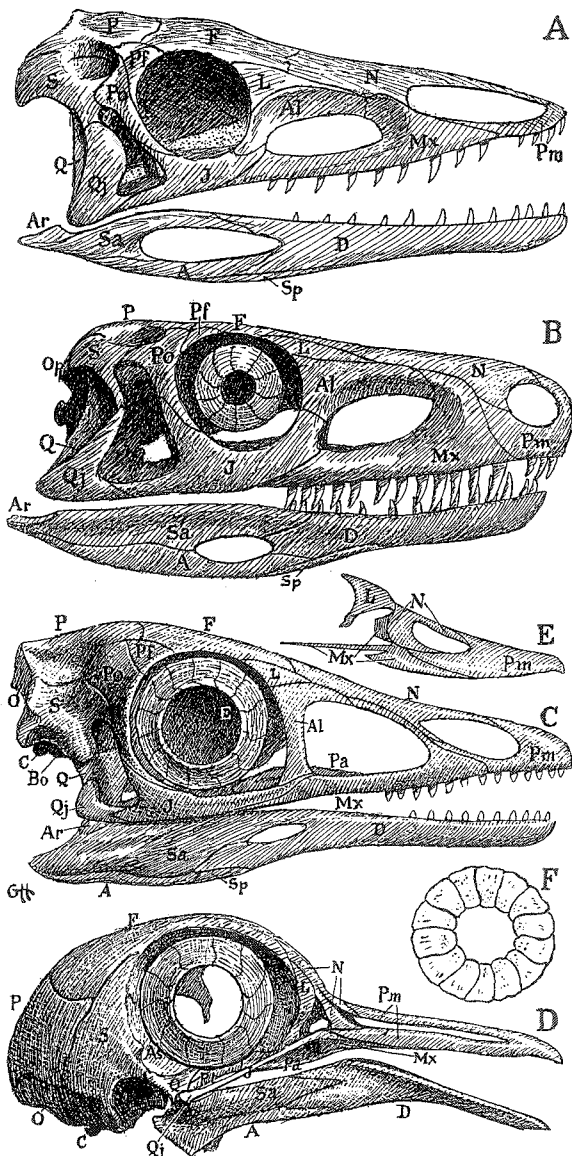
After having studied this remarkable skull I have tried to reconstruct it as shown in fig. 5 C. Certainty in all details is, of course, not attainable; what one regards as a suture, another may ascribe to artefact. Nevertheless, the drawing given here presents a basis for discussion, by means of which we might arrive at more trustworthy results. I have drawn the upper contour a little lower, as the skull, due to compression, has no doubt been raised beyond its natural form. By comparing fig. 5 C with fig. 4, I, anybody can see what I have added.

Fig. 5. Right side-view of the skull A of *Aëtosaurus ferratus* from the Triassic, after F. v. Huene; B of *Euparkeria capensis* from the Triassic, after R. Broom; C of *Archaeornis siemensii*, restored and drawn from a plastic model after the drawing in fig. 4, I; D of Pigeon (*Columba domestica*); E upper jaw of Pochard-duckling (*Fuligula ferina juv.*); F sclerotic ring of *Thalattosaurus alexandræ* from the Triassic, after Merriam. Al adlachrymal, C occipital condyle.

Fig. 5 shows also the skulls of two fossil reptiles, the Pseudosuchians *Aëtosaurus* and *Euparkeria*, as well as that of a pigeon, so that their mutual resemblances and differences may be easily traced.

Aëtosaurus is drawn after F. v. Huene (6), but as his reconstruction in profile also shows P, F, N, and the supratemporal vacuity, seen from above, I have, in my drawing, altered this as well as possible from his figures 2—18. Likewise the suture between J and Mx is drawn from his fig. 10. From the drawings by Broom (7) I have formed a plastic model of *Euparkeria*, and from this, figs. 5 B and 6 A are drawn.

Following Dames, it has been emphasized in all the descriptions of *Archaeornis* that its skull is that of a true bird. I do not concur in this opinion. On the contrary, I think the resemblance to that of a reptile is much more pronounced than to that of a recent bird. The only bird-like feature seems to be the large orbit, but nearly the same thing is to be found in many Pterosaurs (*Rhamphorhynchus* and *Campylognathus*) and in Dinosaurs (*Anchisaurus*, *Compsognathus*, and *Struthiomimus*). A large preorbital fenestra, too, occurs in



both the oldest Pterosaurs from the Lower Lias (*Dimorphodon*) and in the later ones from the Cretaceous (*Ornithodesmus*).

With regard to the teeth, it is difficult indeed to imagine a bird without a beak! But the insertion of these teeth in the premaxillary makes it equally certain that this unique being was furnished with no beak. But this is entirely at variance with our conception of a "genuine" bird. The teeth, too, are in all respects true reptilian teeth. Likewise are the short premaxillary and the far forward lying narial aperture in general conformity with corresponding features among the reptiles. The recent bird, on the contrary, has a greatly prolonged premaxillary; in the pigeon it forms the whole upper beak (see also fig. 3). Nevertheless it is remarkable that the sutures between Pm, N, and Mx have preserved their mutual relationships right down to the present time. One might think that I had drawn this part of the skull of *Archaeornis* from that of *Euparkeria*, instead of which the sutures are taken from those of the beak of the little Pochard-duckling (fig. 5 E); in the pigeon too, the above-mentioned sutures are still as in the reptile.

A long and slender bony bridge, absolutely characteristic of the bird, is formed by Mx, J, and Qj (see also fig. 3). But look at these three bones in *Archaeornis*! There is here not the slightest resemblance to those of a bird. The jugal especially looks quite different from that belonging to a "genuine" bird. It grows broader posteriorly, and a little behind the middle of the orbit its breadth increases so considerably that a firm connection with the postorbital may be supposed, although this bone is not preserved in the fossil. The entire form of the jugal with its three tapering points, proves it to be a true reptilian bone. Nor is the maxillary in the slightest degree bird-like, which also holds good of the quadratojugal. That the skull of *Archaeornis* might have been akinetic is mentioned above.

Moreover, judging from the position of the quadratojugal in its relation to the squamosal, we may safely conclude that these bones in the ancestors of *Archaeornis* have been in contact as in reptiles. Further, the frontals are reptilian, in as much as they have not as yet attained the enormous expanse occasioned by the large brains in recent birds. This is best illustrated in fig. 6.

My readers may think it rather bold to draw the skull of *Archaeornis* as seen from above, this view not at all presenting itself in the fossil. When from the profile we undertake to make a plastic model of the skull, however, we are bound also to get some idea of it in dorsal view. The only uncertainty obtains with regard to the breadth of the skull posteriorly, but this is rather immaterial for our investigations.

Now we find that the two frontals in *Archaeornis* have nearly the same position as in *Euparkeria*, while in the pigeon they have broadened and increased to such an extent in the rear as to push the parietals entirely down on the back of the skull, though these are also very much enlarged. — Seen from above, the difference between the skull of *Archaeornis* and that of *Euparkeria* is still more conspicuous than in profile; that of *Archaeornis* is obviously on the way to become a bird's skull. In dorsal view, the supra-

temporal vacuities are also seen to better advantage; these, of course, are amongst the most doubtful features. If they are present, as I have supposed, they must have been rather narrow and fissure-like, starting to dis-

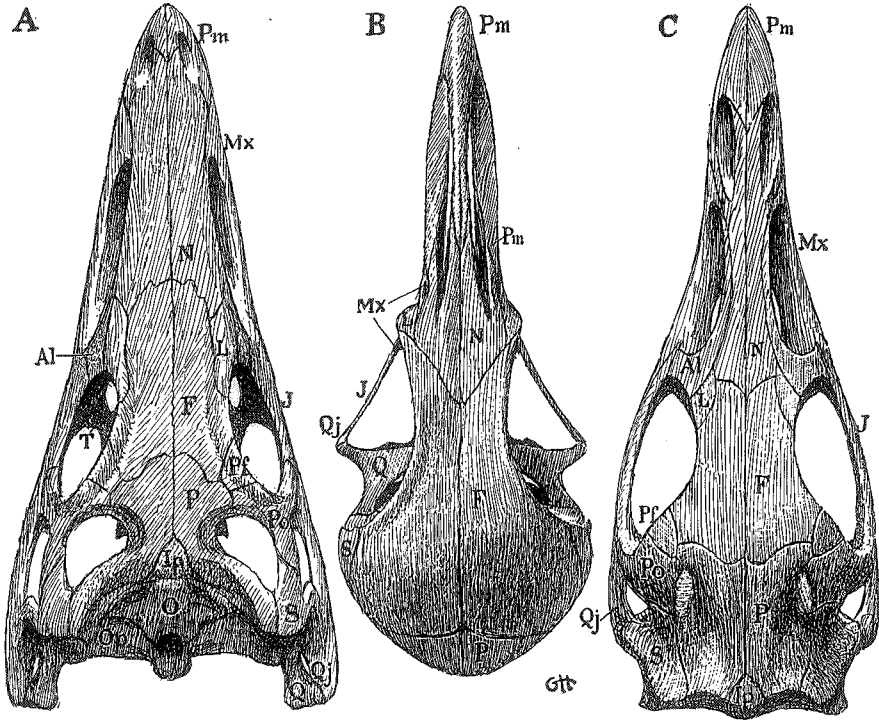


Fig 6. Skull in upper view A of *Euparkeria capensis*, after Broom, B of Pigeon (*Columba domestica*), C of *Archaeornis siemensi*, by the author, restored and drawn from plastic model.

appear where the braincase begins to expand. — The facts in regard to the temporal hole, as found in more recent birds, will be mentioned in Part III (figs. 80 and 81).

Altogether, the skull of *Archaeornis* might very well belong to a reptile, but decidedly not to a recent bird.

The vertebræ and ribs. Dames (2) states that the plane between two vertebræ is to be seen as a straight line, thus showing that the articular surface was not saddle-shaped. Both Marsh and Dames think the surfaces biconcave. I have not been able to verify this, no articular surface being exposed in the fossil. As biconcave vertebræ, however, are found in *Ichthyornis* of the Cretaceous epoch, the vertebræ of *Archaeornis* had most likely the same shape. This feature evidently points towards lower forms (19).

The spinous and transverse processes seem to be slightly developed. The spinal column is composed of 10—11 cervical, 11—12 dorsal, 2 lumbar, about 4 pelvic, and 20—21 caudal vertebræ. The surfaces of the vertebræ, unfor-

tunately, are badly preserved; therefore I have not been able to make a trustworthy drawing of any of them.

The cervicals bear short free ribs, and the thoracic ribs are long, slender, and not in the least bird-like. They have, moreover, no uncinatè processes, which is very strange, these being found in such early forms as the Stegocephalians from the Permian.

Hitherto scientists have been unable to explain these facts, and their statements throw no light upon the problem. Dames (2) says in regard to the ribs that they are not like those of a bird, but on the other hand entirely lack the resemblance to the ribs of any reptile whatever ("wie sie bei keinem lebenden oder fossilen Vogel sonst bekannt sind so fehlt anderseits auch jede Aehnlichkeit mit den Rippen irgendwelchen Reptils"). Wiedersheim (5), on the contrary, asserts that the ribs are slender, rounded like those of the lizards ("Die Rippen der *Archaeopteryx* waren noch schlank, rundlich, ähnlich wie bei Eidechsen"). Lydekker (8) finally states: "In the absence of hooklike (uncinatè) processes to the ribs, *Archaeopteryx* appears to be more specialized than ordinary birds, seeing that these elements exist in many reptiles". The development of the embryo suggests, as we shall see in Part II, that the uncinatè processes in the Jurassic birds were still cartilaginous and, for that reason, not preserved in the fossils.

Still more reptilian than the thoracic ribs are the 9—10 pairs of ventral ribs. No recent bird has abdominal ribs, but they are found in *Hatteria* and in Crocodiles. They have nothing to do with the axial skeleton, and are developed in the embryo without cartilaginous preformation. In other words, they are dermal bones, which arise by direct ossification of a membrane, and in the evolution of species (phylogeny) we may imagine their development from the ventral armour of the Stegocephalians, which was composed of slender, bony rods, converging in front and meeting in the middle line of the belly. These dermal ribs were subsequently transformed into the ossified ventral ribs met with in many fossil reptiles. Two specimens are seen in fig. 7.

The ventral ribs of *Archaeornis* evidently lie, for the most part, in their natural position; only a couple of them are dislocated. As in reptiles, they meet in the middle line at angles which, anteriorly, are rather acute, about 45°, while they become more obtuse posteriorly, nearly 90°. The corresponding angles in the two reptiles in fig. 7 are 60° and 90° respectively. A greater conformity is not to be expected. In *Teratosaurus*, especially, it is plainly discernible that the ventral ribs were not coalesced in the middle line, and that no odd bone was present (9). Exactly the same thing was the case with the ventral ribs of *Archaeornis*. The entire character of these thin and delicate bones, as also their extensive reach, from the pelvis to the shoulder-girdle, indicates that they could not have been sternocostals; nor would they have been preserved in their present condition, meeting in the middle line, had they been fastened to the comparatively broad sternum of a bird. In that case they would have been dispersed by its removal.

Strange to tell, no sternum is found in either of the two fossil birds from the

Jurassic. What Dames thought to be the sternum, is rather formless, and it is difficult to imagine it the remains of a bone (19).

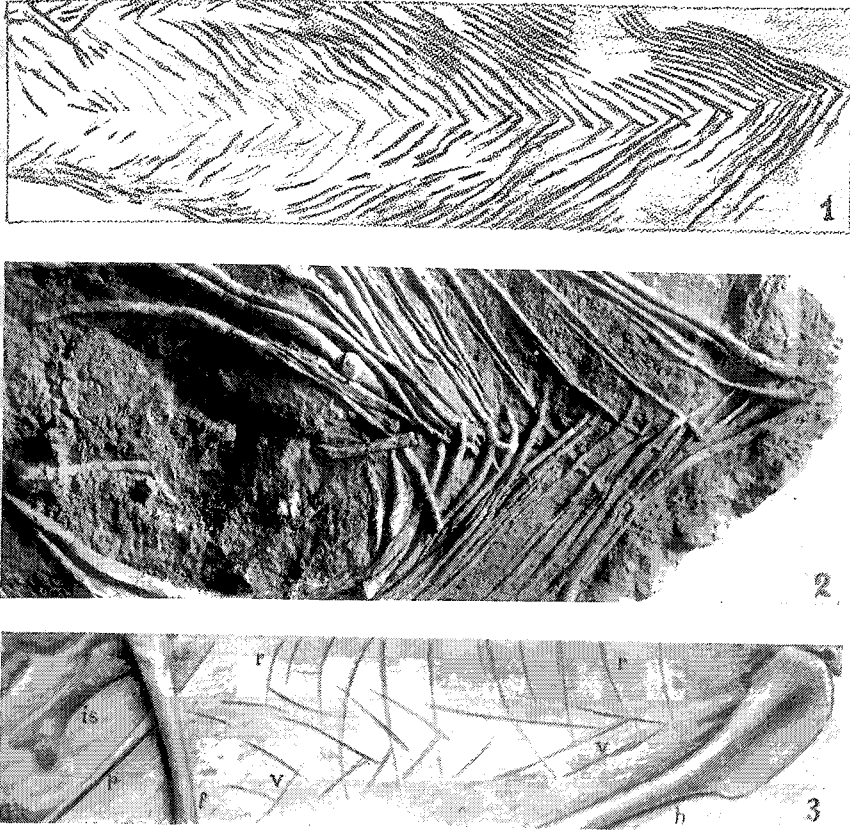


Fig. 7. Ventral ribs 1 of *Kadalisosaurus priscus* from the Permian, after Credner, 2 of *Teratosaurus suevicus* from the Upper Trias, after F. v. Huene, 3 of *Archaeornis siemensii*, original drawing by the author; f femur, h humerus, is ischium, p pubis, r ribs, v ventral ribs.

The shoulder-girdle. The two scapulæ of *Archaeornis* are seen in fig. 2, and near their foremost ends the tops of the two coracoids are protruding, but they are not yet fully uncovered. At the proximal end of the left humerus, a piece of the clavicle appears, and some small pieces of this bone are also to be found on the back of the slab, together with the distal end of the left coracoid (Dames).

The information to be gained from these particulars is but slight, but, fortunately, in *Archaeopteryx lithographica* the whole form of the right coracoid is uncovered, connected with the scapula. This coracoid bears some resemblance to that of the ratite birds, a fact that does not go to prove that *Archaeopteryx* is more closely related to these than to the Carinates. The Ratites have only retained more of the primitive features. The coracoid in

Hesperornis (fig. 8 H) shows some of the same characters, but in the rest the resemblance is small.

The most remarkable feature of the coracoid of *Archaeopteryx* (fig. 8 A) is the presence of two indents on its inner border. According to Petronievics (4) these are probably homologous with the fenestræ in the coracoid of the lizards (*Lacertilia*). He gives no illustration, and hence in fig. 8 C, I have remedied this omission on his part. These fenestræ lie between the osseous and cartilaginous parts of the coracoid, and when we imagine the cartilaginous part, or precoracoid, cut away, there is no denying that some resemblance is to be found. A small foramen in the upper part of the bone is also present in reptiles (fig. 8 E); it is likewise seen in the coracoid of *Hesperornis*.

"Although *Archaeopteryx* was obviously a bird of flight, its scapulo-coracoid is more closely similar to that of certain Mesozoic reptiles than that of any other known bird" (3). In the scapula we ought to notice that "its proximal end bears a well-developed acromial process, from which a very thin lamina of bone extends to the coracoid, forming the floor of a hollow in which the furcula evidently articulated" (3). The same is the case with the scapula of *Archaeornis* (2), and this is a pronounced reptilian feature, because the clavicle in reptiles always runs from the scapula to the episternum (fig. 8 C and E). Part II will show us that this also is found in the embryo of birds, the keel (crista sterni), with which the clavicle is in contact, being simply the homologue of the episternum of the reptiles (see figs. 68 and 69).

In *Hesperornis* (p. 42) the clavicles are preserved (fig. 8 H), and Marsh (10) says concerning them: "The clavicles of *Hesperornis* are separate, and are unlike those in any recent adult bird, although they strongly resemble the corresponding bones in some embryonic forms". As late as the Lower Miocene, well separated clavicles are to be found in adult birds (fig. 69, 2), and in the bird-embryo a clavicle is preformed on each side as in reptiles. We are thus entitled to expect well separated clavicles in *Archaeopteryx*. Consequently, it is difficult for me to believe that the bone which is interpreted as the furcula (merry-thought), really represents the fully coössified clavicles. The great number of rather primitive features, found in the skull, tail, pelvic arch, hand, and foot, also testify against it. In fig. 8 A, I have therefore only indicated this "furcula" by a dotted line. If an episternum had been found in *Archaeopteryx*, it would not have been surprising, as a preformation of this bone is present in the bird-embryo (figs. 68 and 69).

We may take it for granted that *Archaeornis* had a breastbone, but it is rather difficult to understand how there could be sufficient room for such a thing. The distance from the proximal end of the right scapula to the angular point of the first pair of ventral ribs is no greater than the height of the coracoid, and consequently there could not have been much space for the sternum. That it was broad, is indicated by the articular surfaces of the two coracoids. In fig. 8 A, I have drawn it as I imagine it to have been. As all its surroundings apparently lie in place, it seems improbable that some beast

of prey had taken it away and eaten the flesh, but possibly it was cartilaginous as in reptiles. This, however, seems to clash with the fact of the well-developed

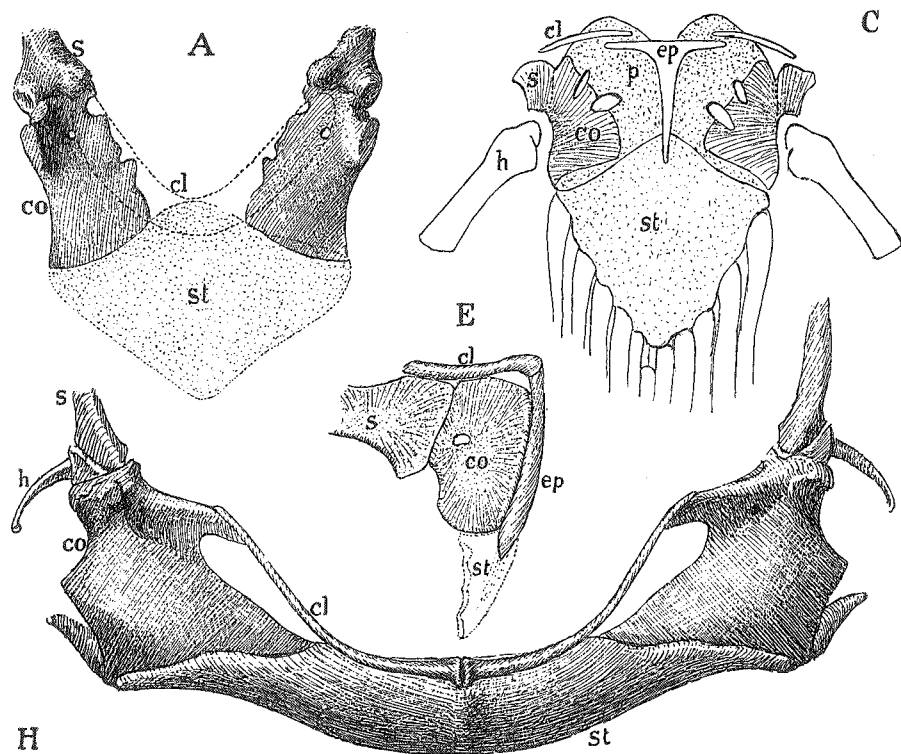


Fig. 8. Shoulder-girdle and breastbone of A *Archaeopteryx*, C *Carsosaurus* from the Cretaceous, after Nopcea, E *Euparkeria capensis*, after R. Broom, H *Hesperornis regalis* from the Cretaceous, after Marsh; cl clavicle, co coracoid, ep episternum, h humerus, p precoracoid, s scapula, st sternum.

remiges, which would require powerful muscles on the breast. Here is a puzzle, which, it is to be hoped, fresh discoveries will be able to solve.

The pelvis of *Archaeornis* is reproduced in fig. 9 III. The contour of the ilium is rather doubtful, the tip of its posterior end being broken, while the anterior part of the preacetabular portion is wanting, the bone and the damaged surface of the lumbar vertebræ apparently running into each other. Nor can the dorsal outline of the ilium be drawn with absolute certainty, imperfect as it is. Furthermore, a jagged line of fracture (f) crosses the bone horizontally; just above the acetabulum it merges into the dorsal edge, a little below which it runs. The lower part of the preacetabular portion seems to be covered with an indeterminable mass (x) in projection of the pubis. — The drawing of the pelvis by Dames is inaccurate, which may be seen in fig. 10 A, where the outline of my drawing is compared with that of Dames's, the two acetabula coinciding.

The outer face of the ilium is concave, but slightly convex above the acetabulum, like that of *Archaeopteryx*. In fig. 9, I, I have drawn the pelvis of *Archaeopteryx* in the same light as III, for better comparison. If the ilium of *Archaeornis* were intact, there would be a close resemblance between the two ilia, and in shape they are very much like the ilium of *Ornithosuchus* (fig. 10), the postacetabular part being more perpendicular (fig. 12, 1 and 2) than this part in recent birds which constitutes an absolute dorsal surface (figs. 10, 12, and 13 ds).

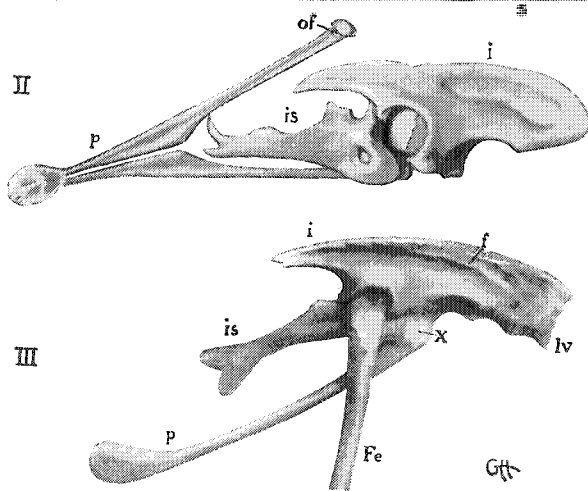
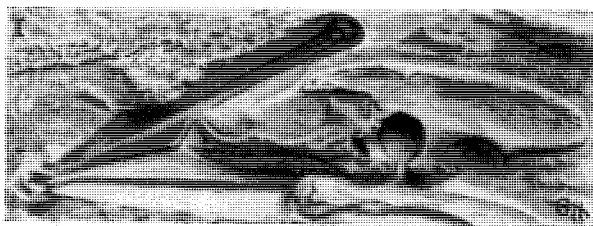
The ischium of *Archaeornis* has evidently a form differing from that of *Archaeopteryx*. Its distal end has two broad prominences, while that of *Archaeopteryx* bifurcates into two distinctly separate processes, the upper one of which curves upwards. The drawings show the differences, but some caution in comparing them is necessary, because the preservation (or the preparation) of the ischium of *Archaeornis* is not good, and in some places the surface of the bone is wanting. The ischium lies a little deeper in the stone than the pubis, but there can hardly have been an ischia-symphysis. The bone seems to be displaced anteriorly, its proximal part obviously lying below the femur, so that a possible foramen, found in the ischium of *Archaeopteryx*, is not visible.

The ischium of *Archaeopteryx* has a shape so peculiar that it seems to be entirely dissimilar to that of either birds or reptiles; possibly a cartilaginous supplement made the irregular outline more even. The proximal quadrangular process on the upper border bears some resemblance to that on the ischium of *Lacertilia* and *Sphenodon* (Petronievics 4). The bone "bends inwards at the distal end" (3), but this is not discernible in the illustration furnished by Petronievics and Woodward (fig. 9 II), where, moreover, the ischium is too broad in the middle. As a matter of fact, the bone bends first outwards and then inwards, but as this is difficult to show in a side view, the dorsal aspect in fig. 12, 2 gives due credit to the curvature. But the planes of the proximal and distal parts of the ischium, too, are turned in different directions, the bone being twisted in the middle. To show this I have drawn the pelvis, in fig. 9, I, from an excellent plaster cast, kindly supplied by the authorities of the British Museum. Perhaps the entire form of the ischium will be best understood from fig. 13, A, bottom figure.

This curving of the distal part of the ischium is to be found in reptiles in consequence of their ischia-symphysis (fig. 13, O), but it is the reverse of that of the ischium of a recent bird (fig. 10, F; cf. also fig. 12, 2 and 3 and fig. 13, A and L). In *Archaeopteryx* this inheritance from a reptilian ancestor may still be traced in spite of the considerable dilatation of the pelvis at the back and the disappearance of the ischia-symphysis, which is most likely due to the laying of larger and fewer eggs with a solid shell. By measuring the depth at which the distal end of the ischium lies, we learn that the two bones did not meet in the median line, and consequently there was no ischia-symphysis.

The pubis of *Archaeornis* is well preserved in the part lying behind the femur; in front of the femur the bone is partly obscured, and by a comparison

Fig. 9. Pelvic girdle of I *Archaeopteryx lithographica*, drawn from a plaster cast of the pelvic region, provided by the British Museum. II *Archaeopteryx lithographica*, after Petronievics and Smith Woodward, III *Archaeornis siemensii* from original drawing by the author. Fe femur, f line of fracture, i ilium, is ischium, l lumbar vertebrae, of obturator foramen, p pubis, s scapula, x indeterminate mass.



with that of *Archaeopteryx* (fig. 9) one gets the impression that this piece mainly consists of the lower part of the preacetabular portion of the ilium, and does not belong to the pubis. But the broken surface (x) makes it impossible to be positive in our conclusion.

It is most fortunate that recently the pubes of *Archaeopteryx* have been uncovered (3), these being an important addition to our knowledge of the pelvic arch. They meet without fusion in an extended symphysis (fig. 9, II), and an obturator foramen (of) is to be found in the proximal, articular end of the bone (Petronievics 4*). A symphysis of the pubes (figs. 12, 5 and 13, O) is common in reptiles, and also a foramen in the pubis proper (fig. 10 C). Whether these features were present in *Archaeornis* or no, cannot be decided, as the bone is seen in profile, and the symphysis, if present, is still covered by the stone. According to Petronievics (4), the pubis takes part in the rim of the acetabulum only from the inside, and this would be considered a reptilian feature, the pubis in birds generally constituting the lower part of the acetabular rim (fig. 10 E). If this be correct, it deserves notice that in Cotylosaurs, Pelycosaurs, Theriodonts, Parasuchia, Pseudosuchia (fig. 13, O), Dinosaurs, and Pterosaurs, the pubis is to be seen on the outside of the pelvis, forming the lower-anterior rim of the acetabulum.

The pubis of *Archaeornis* is directed somewhat more backward than in the illustration by Dames, and consequently forms a more acute angle with the ilium (fig. 10 A). The above-mentioned displacement of the pelvic bones shows that these were not fused together as in recent birds, but "the bones were evidently all separate" (3), as in reptiles.

As a whole, the pelvic arch of the two Jurassic birds presents but very slight resemblances to those of recent birds; the three elements have not yet

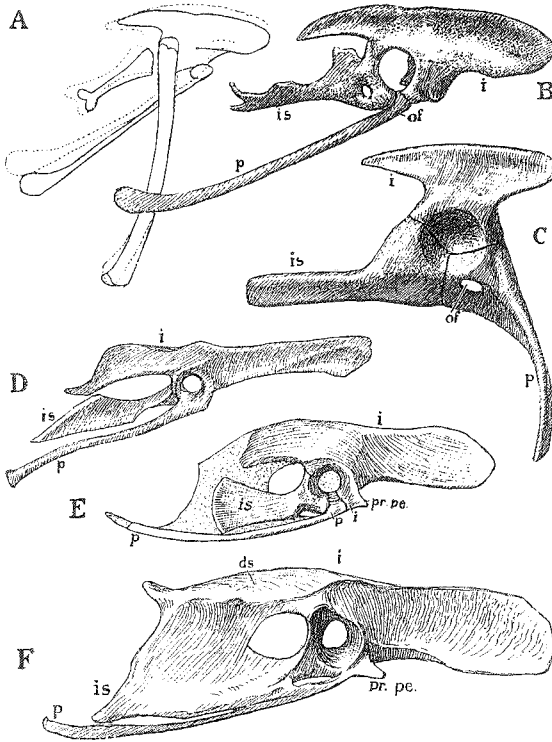


Fig 10. A outline of the drawing by Dames (full line) of the pelvis of *Archaeornis* compared with that by the author (dotted line) of the same pelvis, B restored pelvis of *Archaeopteryx*, pelvis of C *Ornithosuchus woodwardi*, after R. Broom, D *Apatornis* from the Cretaceous, after Marsh, E chick of Pea-fowl (*Pavo cristatus*), F Hen; ds dorsal surface of ilium, i ilium, is ischium, of obturator foramen, p pubis, pr. pe. pectineal process.

attained the strongly marked shape found in the latter. The nearest approach to the general form, we find among the Ratites (fig. 11), but no obturator foramen is found in the pubis proper of these, and the pelvic bones in old birds are coalesced to each other and to the sacrum. In the other modern birds, the ilium, as a rule, has grown together with the ischium

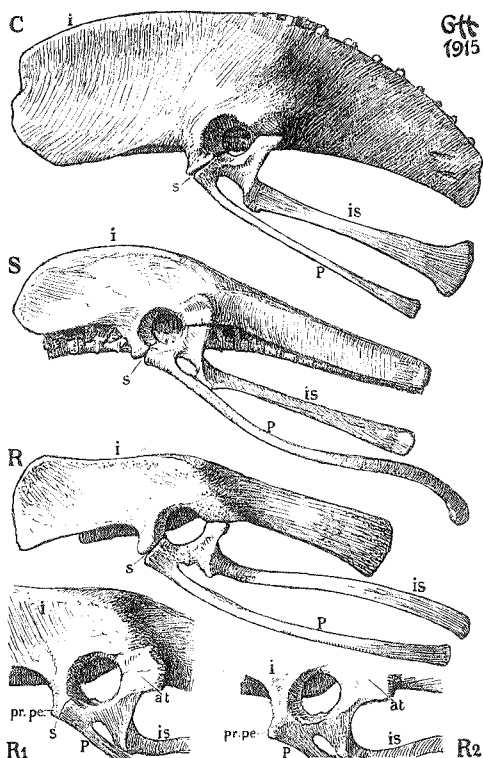
behind (fig. 10 F), and a foramen in the ischium is not present, any more than an obturator foramen in the pubis.

In some groups of recent birds, a prominence on the pelvis is seen in front of the acetabulum; it is called the pectineal process (*processus pectinealis*, fig. 10 F pr. pe). Only in comparatively few birds, e. g. *Ratitæ*, *Galliformes*, and *Coccygomorphæ*, do we find this process boldly defined, and amongst the last mentioned group, *Turacus* especially has a very conspicuous one, much more pronounced than that of either *Ratitæ* or *Galliformes*. These very facts suggest that this process is either a new formation, occurring sporadically, or a relic from the past, still persisting in some birds of the present time.

Owing to the close investigations of the embryos of a very great number of birds, by Lebedinsky (11), we now know that the first alternative is correct, not the second. In embryos of birds with no pectineal process, there is no indication of it at all; while e. g. in the seven days old embryo of *Gallus* the same thing is true, but it makes its appearance on the eighth day, and from that time increases constantly during the embryonic development of the bird. No retrogradation occurs, from which fact we may conclude that this process is no relic from the past. The pectineal process always originates from the ilium, never from the pubis. We need not go to the embryo to see this, any chick will show the same thing (fig. 10 E).

In adult birds the degree of development of this process depends upon the

Fig. 11. Three pelves of young Struthious birds, C Cassowary, S Ostrich and R Rhea; R₁ the part around the acetabulum of a young but full grown Rhea, R₂ the same of an old Rhea; pr. pe. pectineal process, s suture between ilium and pubis.



ambiens muscle, which, according to the investigations by Gadow (Bronn: VI, Vögel) is attached to it and has to do with the mode of locomotion of the bird.

It is, therefore, noteworthy that no pectineal process is to be found on the pelvis of *Archaeopteryx*; it does not belong to the primitive bird-pelvis, and this fact confirms the results derived from our embryonic observations. Fig. 10 D goes to prove that this process did not occur in birds from the Cretaceous period either.

I emphasize this fact so strongly because, to some scientists, this pectineal process has served as a point of departure for their conjectures:

that birds are developed from some highly specialized reptiles (*Ornithischia*), the pubis of which, posteriorly directed, has a large prominence in front, homologous with the pectineal process in birds. As this process, however, belongs to the ilium, the pelvis of Struthious birds was resorted to, the pectineal process in these, it was urged, being seated on the pubis.

My fig. 11 shows that this is by no means the case. The sutures between the two bones in young birds are discernible, and further, in the old Rhea, the point of the pectineal process proves to belong to the ilium.

The reconstruction of the pelvis of *Archaeornis* in fig. 23 is so made as to allow the pubis and the ischium, both of which seem to be dislocated in the fossil, being thrust forward too much, to be drawn a little further back.

The os sacrum, the coalesced vertebræ supporting the pelvis, also differs greatly from that of recent birds. As mentioned before, the pelvis of *Archaeornis* had scarcely more than 4 vertebræ. When we take into account the length of the preserved lumbar vertebræ compared with the rather short ilium, there can have been no more; I have even shortened the vertebræ a little in fig. 12, 2. Besides, from the position of the tail, it is plain that the hindmost pelvic vertebra, in all probability, was seated a little behind the acetabulum. No bird has so few pelvic vertebræ; the minimum is 11, but in some birds the number reaches 23.

On the other hand, this small number of vertebræ, loosely connected with the pelvic bones, is an undoubted reptilian feature. The usual number of pelvic vertebræ in reptiles is 2; *Ornithosuchus* had 3 (fig. 12, 1), *Dorygnathus* 3—4, and *Rhamphorhynchus* 4; but in Pterosaurs from the Cretaceous it was as large as 10, and these were coalesced (*Pteranodon*). Among Dinosaurs, too, the number was changing; the Sauropods had 4—5. *Iguanodon* 4—6, *Corythosaurus* 8, and *Claosaurus* 9.

Thus knowing the primitive bird-pelvis with tolerable certainty, we are able to reconstruct a model of it. The acetabular breadth of the pelvis in *Archaeopteryx* is indicated by the distance between the proximal ends of the two pubes, and from the approximation of the preacetabular part of the ilium to the lumbar vertebræ we may infer that the transverse processes of the first pelvic vertebræ were but small. According to Petronievics (4), the proximal end of the right pubis of *Archaeopteryx* lies in place between the ilium and the ischium; but the pubic symphysis, being seen from above, while the ilium and ischium are in profile, shows the two pubes in a position that cannot be natural. If this be taken into account, the entire appearance of the pelvis must approximately have been as shown in figs. 12 and 13.

Archaeopteryx was of the size of a common fowl. In fig. 12, therefore, I have placed its pelvis beside that of a medium-sized hen, and at a glance we see how small, weak, and primitive it was. Both pelvises are of nat. size, but the pelvis of *Archaeopteryx* is not even half the size of that of the hen. The comparison is so amazing, nay almost incredible that it is hard to believe that the proportions are correct. But they are, to be sure! In this way we get a good idea of the development through which the bird-pelvis has passed in the course of time. We see how the individual elements, from being loose and weak in their build, have encroached upon the lumbar and caudal vertebræ, forwards and backwards respectively, and united in the strongly built form of the recent bird-pelvis. Even if we suppose that the sacrum of *Archaeopteryx* was composed of 5 or 6 vertebræ, the whole character of the pelvic arch is nevertheless very different from that of a hen. Its position seems to be nearly half-way between that of the bird and that of the reptile, perhaps a little nearer to the latter. Though the pubic symphysis in the reptile is directed forward, yet the symphysis is found in both *Archaeornis* and the reptilia, but not in recent birds, and in Part II we shall see that the pubis of the bird-embryo, in its preformation, is also directed forward. — Knowing the width of the pelvis of *Archaeornis* behind, we are able also to indicate the approximate size of its egg (fig. 12, 6); its content was scarcely a quarter of that of a hen.

Fig. 13 gives a better conception of the three-dimensional proportions of this peculiar pelvis, when placed side by side of that of the Pseudosuchian.

The hind limb is far from being so bird-like as it has often been urged. It has been alleged that the only difference from that of a modern bird is that the fibula of the *Archaeornis* had the same length as the tibia, but, for the rest, the tarsus and metatarsus were exactly like those of recent birds. This

is not the case at all, for the hind-limb is in several ways so primitive that we must go to the bird-embryo, nay almost beyond this, to see anything like it.

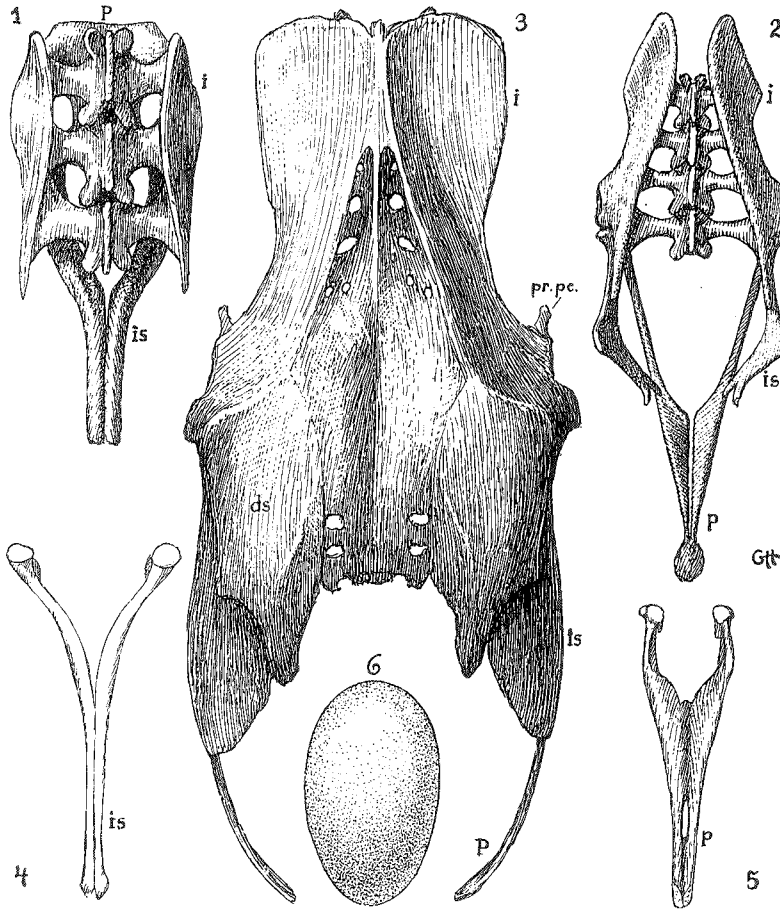


Fig. 12. Restored pelvis 1 of *Ornithosuchus woodwardi* from the Triassic, and 2 of *Archaeopteryx*, drawn from plastic models, the last one also from a plaster cast of the fossil, both in dorsal view; 3 pelvis of a Hen, dorsal view, all nat. size; 4 ischiasymphysis of *Dryosaurus altus*, after Marsh; 5 pubic symphysis of *Coelurus agilis* from the Upper Jurassic, after Marsh; 6 nat. size of egg of *Archaeopteryx* in accordance with the width of its pelvis; ds dorsal surface of ilium, pr. pe. pectineal process.

It is a well known fact that we see nothing of the tarsus as such in an adult bird, three of the proximal tarsals, viz. tibiale, centrale, and intermedium, fusing with one another and with the distal end of the tibia. The fourth proximal tarsal, the fibulare, too, fuses with the tibia, forming the outer condyle. The result is a bone consisting of tibia plus half the tarsus, hence called "tibio-tarsus".

The five distal tarsals fuse at an early stage into one cartilaginous mass,

in which only one centre of ossification appears, and then it fuses with the proximal ends of the second, third, and fourth metatarsals, which also have grown together, and this bone, consisting consequently of half the tarsus plus the metatarsus is called "tarso-metatarsus". The articulation of the ankle-joint of a bird, therefore, lies in the middle of the tarsus.

The hind legs of *Archaeornis* are seen on the slab in profile (fig. 2). They are not quite complete, but so much has been freed from the matrix that I have been able to draw the right ankle-joint from the posterior. The drawing is seen in fig. 14 A; a third of the joint is concealed in the matrix, but in C it is reconstructed as a whole. We see but the distal end of the fibula, because the rest has stuck to the upper slab, and the fibulare, which is distinctly separate and not at all fused with the tibia or fibula. Moreover, near the distal end of the tibia there is a transverse furrow, laterally somewhat obscured, and this is possibly the boundary line between the tibia and the three other proximal tarsals. In the young chicken (fig. 14 D) we may find a hint in the same direction.

Another curious feature is that the distal tarsals are not discernible, obviously not lost however, as there is no gap in the joint. The only possible explanation is that the distal tarsals have not fused with one another, but each one separately with the upper end of the corresponding metatarsal, a phenomenon having no parallel among birds, their embryos, or reptiles. The nearest approach to this we find in many Dinosaurs (fig. 109), where the respective distal tarsals are in close contact with the corresponding metatarsals, and yet not fusing with them (19).

A circumstance still more remarkable is that the three metatarsals lie separate beside one another, which may also be seen in fig. 15, 3, where the second metatarsal is broken and a piece of it dislocated. They are not fused together as in adult recent birds, the metatarsals of which are not in the same plane; the upper end of the middle one is thrust backwards in proportion to the others (figs. 14 D and 15, 4). This is not the case in *Archaeornis*, whose metatarsals lie in the same plane as shown in the drawing. Nor is there any ridge on the middle one, as in the pigeon (fig. 15, 4), nor any grooves for flexor tendons.

In *Archaeopteryx*, too, "are the metatarsals separate and appear to be in one plane, but the upper end is obscure" (Dr. A. Smith Woodward in a letter). The photograph of the fossil (fig. 1) shows this very distinctly; so does fig. 15, 2, which is drawn from an enlarged photograph. The three metatarsals 2, 3, and 4 are all discernible; they have the same straight shape as those of *Compsognathus longipes* (fig. 15, 1) and lie perfectly parallel. The separation is also indicated by the fracture of the second metatarsal, this fracture not passing on to the third one. The drawing by Owen (1) is very inaccurate, the tarso-metatarsus being too thin in the middle and thickened at the ends, nor are the metatarsals drawn separated. Dames (2) says that there is a longitudinal line to be seen between them, but he dares not draw the correct conclusion, but thinks that the line is a crack in the stone. — It is a most

important fact that the position and shape of the metatarsals in both Jurassic birds are more primitive than in some reptiles (*Struthiomimus altus*, fig. 126, B).

In fig. 15 we can make a comparison between the left foot of *Archaeopteryx*

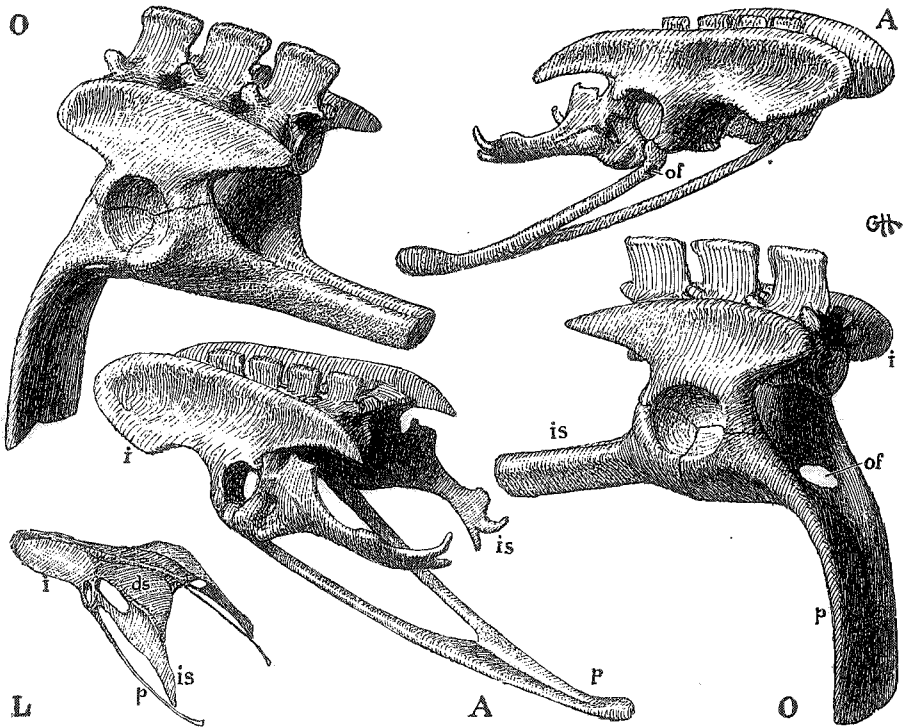


Fig. 13. The pelvic arch and sacrum of A *Archaeopteryx* in two different views drawn from a plastic model, and from a plaster cast of the fossil; O *Ornithosuchus woodwardi*, also drawn from a plastic model, after the reproductions of E. T. Newton and R. Broom; L pelvis of a young Blackheaded Gull; ds dorsal surface of ilium, of obturator foramen.

and *Archaeornis*, and compare them with that of a reptile, and of a modern bird. *Archaeopteryx* was somewhat larger than *Archaeornis*, but its foot, too, was relatively much more powerful. The bones in the foot of *Archaeornis* seem to be weaker, especially the phalanges of the toes, which have a less distinctive shape, and are not so strong as those in *Archaeopteryx*, the foot of the latter having evidently possessed greater grasping power. The first toe of *Archaeornis* is also very short in comparison with that of a perching bird (fig. 15, 4). Still shorter is the first toe of *Compsognatus* and somewhat higher placed, for it had ceased to be functional. In other respects, however, the feet of the Jurassic birds bear a close resemblance to those of the reptile, only they have not retained the fifth metatarsal as has the nimble little Dinosaur. All three, however, having the phalanges of the fourth toe unshortened, are more primitive than *Procompsognatus* from the Trias (fig. 126, A). As mentioned above, a toe-pad is preserved on the third toe. It is seen in longitudinal

section, bounded by a light outline, in which the slightly rough surface and the scales of the skin are distinguishable. For comparison I have also drawn a toe-pad in longitudinal section on the third toe of the pigeon.

Turning now to the fore-limb, we see the feathers forming a wing, but the bony structure supporting this is very far from that of a true bird's wing.

The humerus is shown i fig. 16, II and III, in dorsal and ventral views. It is delicate and weak, and though it bears a long radial crest for fastening of the pectoral muscles, its strength is greatly inferior to the powerful humerus of the Pterosaurs. I have added the figure of the humerus of a *Rhamphorhynchus* to show what a reptile is capable of producing for the support of a wing, but it bears no resemblance to that of *Archaeornis* (fig. 16, I). We also note the difference in size of *Archaeornis* and *Archaeopteryx*, by comparing their respective humeri, while a comparison with that of a common fowl (fig. 16, V), which is but a mean flier, will bring out the fact that the power of flight in *Archaeopteryx* has as yet reacted but slightly on the humerus.

Fig. 17 shows the entire fore-limb compared with that of a pigeon, which is of about the same size as *Archaeornis*. We notice, at a glance, the complete transformation of the bones, especially of the hand, carried out through immense periods of time, so as to form a firm base for the primaries. The elbow-joint, too, is weak; for the articulation between humerus, ulna, and radius, has not as yet attained the close adjustment for restricted motion, and there is no ball-and-socket joint between radius and humerus, as in recent birds.

The carpus, too, is still in a very primitive stage of development, as shown in fig. 18. The primitive carpus of the reptile (E) consists of three proximal elements, radiale, intermedium, and ulnare; also two centralia, and five distal carpals, but as the fifth and fourth digits of more specialized Dinosaurs have disappeared, the corresponding distal carpals, of course, have shared the same fate. In the bird-embryo (A and C) the remaining carpals are distinguishable, but so compressed that "c" and "i" can be made out in dorsal view only, the ulnare and radiale in ventral view, while 1 and 2 of the distal carpals have fused together.

Exactly the same phenomena are found in the carpus of *Archaeornis* (B and D), a most striking resemblance, and it is very different from the carpus of a recent bird (fig. 17), where only two elements remain, a radiale (in reality r + i), and an ulnare (c + u), while the distal carpals have entirely fused with the coalesced metatarsals. The carpus of *Archaeornis* is thus much

nearer to that of the reptile than to that of a recent bird.

The rest of the hand is one of the most

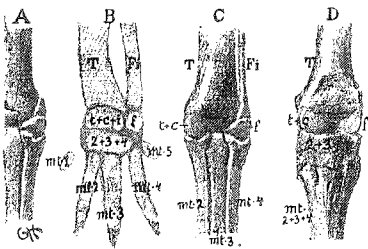
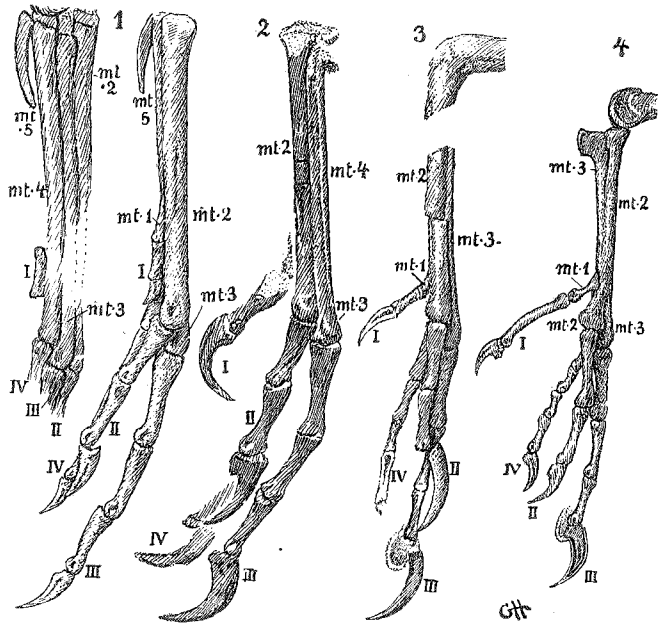


Fig. 14. The right ankle-joint of A and C *Archaeornis siemensii*; A as seen in the fossil, C restored; B embryo of Hen after A. Johnson; D chick, all in back view. Fi fibula, T tibia, c centrale, f fibulare, i intermedium, mt 1—5 metatarsal, t tibiale, 2—4 distal tarsals.

Fig. 15. 1 Right and left foot of *Compsognathus longipes*, a Coelurosaur from the Upper Jurassic of Bavaria, drawn as catoptric images from a photograph of the fossil; left foot of 2 *Archaeopteryx lithographica* drawn from a photograph supplied by the British Museum, 3 *Archaeornis siemensii*, drawn from the fossil in Berlin, 4 Pigeon; mt 1—5 first to fifth metatarsals, I—IV first to fourth toes. 2, 3 and 4 in nat. size.



remarkable features in *Archaeornis*, because the entire reptilian basis still persists, though it sup-

ports the primaries, the impressions of which are distinctly traceable in the stone.

The primitive five-digit hand of a reptile is shown in fig. 18, E. The first digit has 2 phalanges, the second 3, the third 4, the fourth 5, and this digit is the longest of them all. But in all known carnivorous Dinosaurs, a reduction of digits takes place, beginning, as we see in fig. 19, I, from the ulnar side, the fifth and fourth digits having lost two phalanges each. Besides, they are much reduced in size, and the fourth digit is no more the longest, the second one now exceeding it in length, and the clawed phalanx of the first digit has grown much stronger. In fig. 19, II the fifth digit has entirely disappeared, and the fourth is very much reduced. In the hand of *Ornitholestes*, shown in fig. 19, III, the fourth digit is lost, too, only a vestigial metacarpal remains. *Antrodemus* (fig. 19, V) has gone still further, the fourth digit has disappeared completely, and the third is somewhat reduced, being the weakest element of the hand, as in *Ornitholestes* and *Archaeornis*. Even a further reduction of the third digit may occur in Theropodous Dinosaurs from the Upper Cretaceous (*Gorgosaurus*). The specialization of the hand seems to develop along the same lines in Coelurosaurs and in birds, the elongation of the penultimate phalanges, evidently due to special use of the claws, and the shortening of the two proximal phalanges of the third digit in *Ornitholestes*, *Struthiomimus* and in *Archaeornis* being in that respect very remarkable (fig. 19, III, VI and IV). Moreover, I wish to call attention to the greatly shortened first metacarpal in fig. 19, II, III, and V, fully resembling that of *Archaeornis*. The second and third digits of *Ornitholestes* "are closely appressed and incapable of spreading laterally" (Osborn 12) and harmonize, also in this particular, with the digits of *Archaeornis*.

This tridactyl hand of *Ornitholestes* thus bears the most striking resemblance to that of *Archaeornis* (fig. 19, IV) in all details, except that the fourth metacarpal is lost in the latter. This proves beyond a doubt that the three digits of *Archaeornis* are the first, the second, and the third. Several scientists have come to the same conclusion (O. Abel, 12*), and when some embryologists

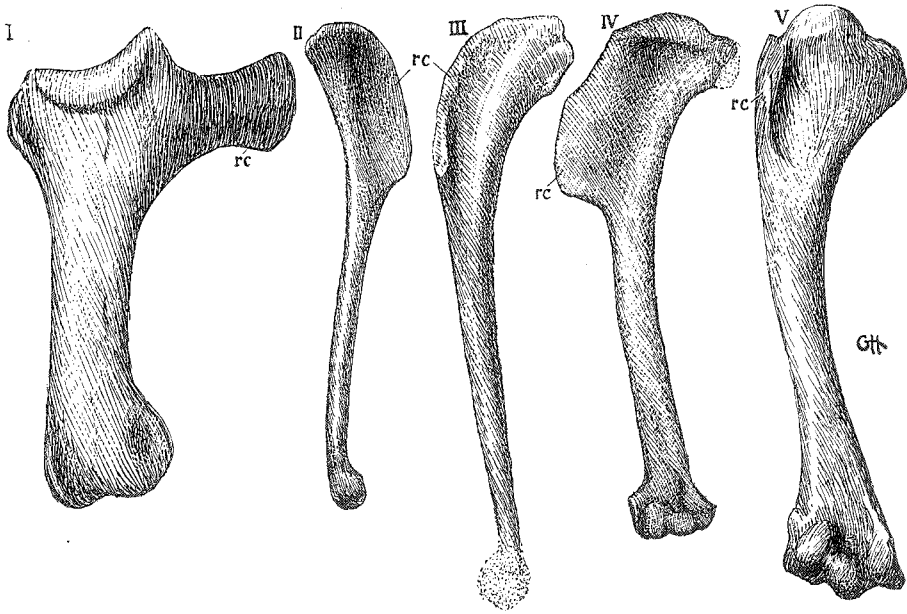


Fig. 16. Right humerus of I *Rhamphorhynchus kokeni*, a Pterosaur from the Upper Jurassic of Bavaria, after F. Plieninger, II *Archaeornis siemensi*, both in dorsal view; right humerus of III *Archaeopteryx lithographica*, after Petronievics and Woodward, IV *Ichthyornis dispar* from the Cretaceous, after Marsh, V Common Fowl, all in ventral view; nat. size; rc radial crest.

have numbered the digits otherwise, it is due to a misinterpretation of details in the embryonic hand, as we shall see in Part II.

That the metacarpals are separate has long ago been alleged by Dames (2), but since then, these bones in illustrations of *Archaeornis* have been drawn so separated that their mobility appeared to be quite unrestricted. Fig. 19 shows the true form of these three metacarpals, and we see that their proximal ends are flattened and compressed in such a way as to preclude any mutual mobility. It is a noteworthy fact that the first metacarpal lies so close to the second that the surface has somewhat encroached upon the side of the latter, and the second and third seem to have fused at their proximal ends. This of course has stiffened the hand considerably.

The two fore-limbs of *Archaeornis* lie nearly in the same position on the slab (fig. 2). This is so strange that there must have been some positive reason for it.

The wing-feathers still adhered to the arm, even when covered with sand and lime-powder, and this of course fixed the position of the bones, but we

may also note that the apparently mobile phalanges of the third digit lie in a similar position in both fore-limbs under the second digit. By examining these phalanges more closely, we observe that on the first phalanx of the second digit in the left hand there is a small prominence (fig. 19, IV p), abutting on the first phalanx of the third digit, evidently to keep the proximal

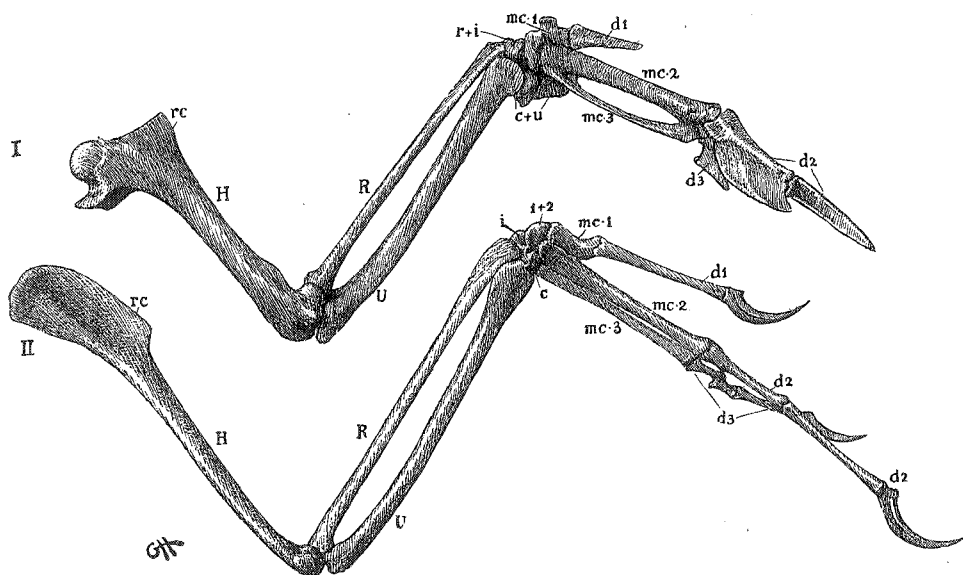


Fig. 17. Right fore-limb of I Pigeon, II *Archaeornis siemensii*, drawn by the author from the fossil in Berlin; H humerus, R radius, U ulna, c centrale, d 1—3 first to third digits, i intermedium, mc. 1—3 first to third metacarpals, r radiale, u ulnare, 1 + 2 coalesced first and second distal carpals.

ends of these two digits in position so as to limit their mobility. In the right hand this prominence is more obscured (fig. 17), but here the joint between the first and second phalanges of the third digit is dislocated, which further suggests that the proximal phalanges of the two digits were immobile. Thus the hands of *Archaeornis* were more rigid than has hitherto been supposed.

The first phalanx of the second digit in the hand of the pigeon (fig. 17, I) is strongly compressed and broadened on the ulnar side, and does not at all resemble the corresponding bone in the hand of *Archaeornis* (fig 17, II), but nevertheless, it is this little prominence (fig. 19, IV) that gives the first hint as to the future dilation of the phalanx.

It has been suggested by some authors that a phalanx in the third digit is broken. Heinroth (13) often mentions "den Bruch des 3. Fingers", but the statement is founded merely upon inaccurate observation. It is a dislocated joint, for the thickened articular surfaces of the phalanges are plainly visible (fig. 19). His further statement: "Der 3. Finger scheint wohl sicher mit seinem

Wurzelglied und vielleicht auch bis zum Abbruchsstelle des folgenden mit dem 2. Finger verwachsen gewesen zu sein“, is also wrong. That this coalescence has not yet taken place in the recent bird (fig. 17, I) is sufficient to disprove it.

Fig. 20 is an enlarged photograph of the left wing of *Archaeornis*. It is taken with strong lateral illumination so as to make the details appear more distinct. The shafts of the primaries are seen as rather deep impressions in the matrix, and they show a slight longitudinal elevation, most prominent at the proximal end. From this we learn that what we see on the slab is a moulding of the under side of the wing, and this corresponds admirably with the fact that the real arm-bones are seen in dorsal view. In *Archaeopteryx lithographica* the impression of both remiges and rectrices, too, are mouldings of the under-side of the feathers, indicating that the dead bird was originally lying on its belly.

The angular position of the hand and forearm shows that the wing is not stretched out to the full extent, and that some of the primaries may be covering others. Dames was able to detect no more than 6 primaries, though anybody can see 7—8 at least. Heinroth (13) thinks *Archaeornis* to be in moult, and he counts 10 primaries, including a feather (probably one of the secondaries) before my No. 1.

In my photograph of the wing, the covered shafts are plainly distinguishable as somewhat darker impressions, and it is easy to trace 11 primaries. That these darker impressions really are due to feather-shafts may be seen in Nos. 1 and 5 showing a proximal dark, as well as a distal light impression. The small one just below the claw is possibly a covert, but most likely a primary; we thus arrive at the very high number of 12 primaries for the most primitive bird we know.

The under side of an ordinary, half-folded wing of a bird shows the shaft of the outmost primary only, while those of the others are covered with the hinder webs of the succeeding vanes. It is remarkable, therefore, that so many shafts are to be distinctly seen in the wing of *Archaeornis*. We may then

imagine the feathers much broader (fig. 20, 1) than they look, with the barbs of the hinder webs overlapping the shafts of the following feathers, which Nos. 8, 9, and 10 in fig. 20 seem to show, but the strong form of the shafts themselves has left an impression on the stone. It is still more remarkable that other feathers, too, show the front web, and

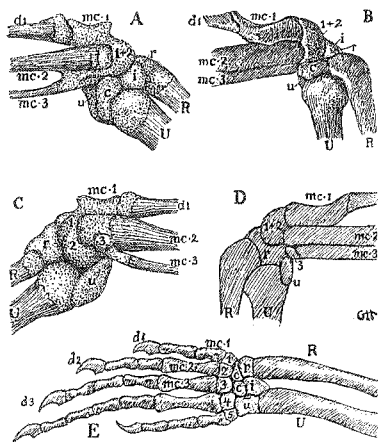


Fig. 18. A and C left carpus of embryo of Hoatzin (*Opisthocomus*), after W. K. Parker, A dorsal, C ventral view; B and D left carpus of *Archaeornis siemensis*, drawn by the author from the fossil in Berlin, B dorsal, D ventral view. E Hand of *Protorosaurus speneri* from the Upper Permian, after H. v. Meyer; R radius, U ulna, c centrale, d fingers, i intermedium, mc metacarpals, r radiale, u ulnare, 1—5 distal carpals.

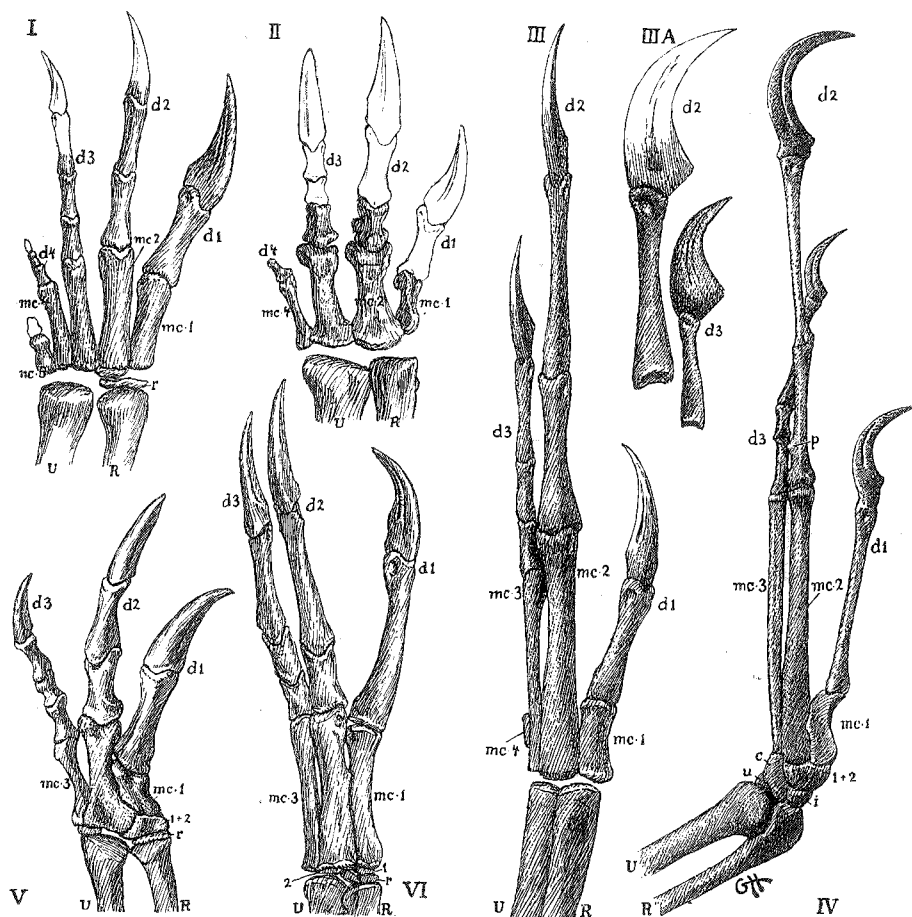


Fig. 19. Left hand in dorsal view of I *Anchisaurus* from the Triassic, after Marsh, II *Ceratosaurus nasicornis* from the Upper Jurassic, after Gilmore, III *Ornitholestes*, a Coelurosaur from the Upper Jurassic, after H. F. Osborn, III A the two distal phalanges of the second and third digits of the same in side view, IV *Archaeornis siemensii*, drawing by the author directly from the fossil, about $\frac{5}{4}$ nat. size, V *Antrodemus valens* from the Upper Jurassic after Gilmore, VI *Struthiomimus altus* from the Upper Cretaceous, after H. F. Osborn; lettering as in fig. 18, p the small prominence, mentioned in the text.

this looks as if a feather might be wanting, rendering it possible that the interjacent darker feather-shafts are marks of feathers not yet full-grown, as Heinroth (13) suggests.

The calami are overlain by the under wing coverts, hence are not visible. When attempting to lengthen the shafts so as to bring them into touch with the arm-bones, we must bear in mind that, since the recent bird has 12 primaries, the first 7 quills, as a rule, are attached to the united metacarpals 2 and 3, the next primary (in this case No. 8) is always borne by the first phalanx of the third digit, while Nos. 9 and 10 are attached to the first phalanx of the second digit, its second phalanx bearing Nos. 11 and 12.



Fig 20. Impressions of the remiges of the left wing of *Archaeornis siemensi* from a photograph by the author; about nat. size. 1—12 the shafts of the twelve primaries, uc under wing covert.

In fig. 21, I have drawn the 12 calami in their right places on the second metacarpal and digit, the eighth one resting upon the first phalanx of the third digit (see also fig. 22, III). The shafts are placed in exactly the same position as the fossil shows. What the primaries of *Archaeornis* looked like, is best seen by comparison with those of a pigeon and of the nestling Hoatzin. The latter is nearest to the hand-wing of *Archaeornis*; or rather, it has still preserved several features of the primitive wing, because the first and second digits are used for climbing purposes. Hence the two last primaries (9 and 10) are retarded in their development, just as the corresponding ones (11 and 12) are shortened in *Archaeornis*.

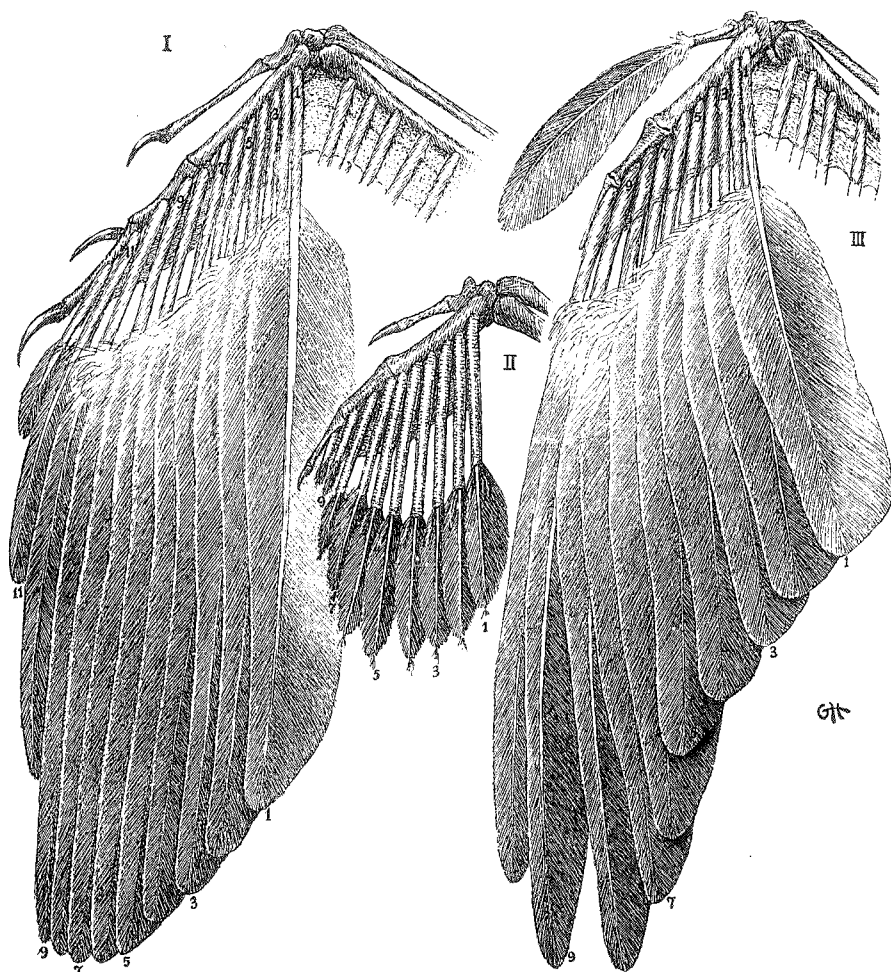


Fig. 21. Left hand in dorsal view of I *Archaeornis* with the primaries drawn in their supposed position on the second metacarpal and digit; the same of II nestling of Hoatzin and III young Pigeon.

There was no alula or bastard wing on the first digit of *Archaeornis*. In the pigeon the clawed phalanx is lost, and the remaining (first) phalanx shows a small excavated groove (also seen in fig. 17, I) for the calamus. Nothing of the kind is discernible on the first digit of *Archaeornis*, nor has the second phalanx of the second digit any excavation for calami, as the corresponding bones have in the pigeon and the Hoatzin, though this phalanx is reached by lengthening the two primaries 11 and 12.

It is self-evident that the claws could be of no use to *Archaeornis* if placed on the digits with the concavity facing forward, as the fossil seems to show. Upon closer examination we find, however, that the claws are not seen in direct profile, but their concavities and points were originally turned towards the under side of the wing, and only the presence of super-imposed chalk-layers has forced them into a lateral position.

A comparison between fig. 19, III A with IV will also show that the ultimate and penultimate phalanges of the digits of *Archaeornis* are not in dorsal view as the rest of the hand; they are seen from the side. The pits at the sides of the distal ends of the penultimate phalanges of *Archaeornis* show this. Consequently the concavity of the claws has not faced forward when the bird was alive.

In fig. 22 I have drawn the expanded primaries and secondaries in both dorsal and ventral views, so that we may form some idea of the position of the three digits between the feathers. Although the three foremost primaries are much shortened, so as to be of no hindrance to the use of the claws, Nature's attempt at producing an organ for both climbing and flying purposes seems to have been anything but successful, and it is not surprising that the grasping power of the wing was lost.

The coverts of the under wing may be traced in fig. 20 uc, and they seem to have been rather long feathers with soft, loose barbs.

We have now examined the most interesting details in the skeleton of *Archaeornis* and have ascertained their much closer resemblance to the corresponding features of a reptile than to those of a recent bird.

This also holds good of the very long tail, which is so absolutely lizard-like that nobody might have guessed that it belonged to a bird, if it had been found isolated and without feathers. This tail is composed of 21 long and slender post-sacral vertebræ, while the 5—8 free post-sacral vertebræ of a recent bird are short and broad, and are followed by a large subtriangular upright plate, the pygostyle (fig. 23, py), which the embryo shows us to be formed by the fusion of 6—10 vertebræ. But in a recent bird the size of the very elongated sacrum is partly due to the annexion of 5—6 originally caudal vertebræ. Thus the bird has, as a matter of fact, preserved nearly the same number of post-pelvic vertebræ as *Archaeornis*.

The five anterior tail vertebræ in the Jurassic birds could scarcely have borne rectrices, and it is uncertain whether the sixth, seventh, and eighth did, but each of the remainder had a feather on either side, and thus the number of tail-feathers was an even one. This is best seen in *Archaeopteryx* (fig. 1), the tail of which ends in two feathers; in *Archaeornis* the end of the last rectrices is wanting.

In recent birds the tail-feathers also grow in pairs; normally an odd number is never found, and thus we here find another legacy from the ancient bird, but while the tail of *Archaeornis* approximately resembles a feather-ribbed leaf, the tail of modern birds is fan-shaped.

In order to invest the tail of *Archaeornis* with sufficient rigidity during flight, the vertebræ are connected with ossified tendons; nevertheless, it was obviously an awkward steering gear, however, since it has undergone a complete transformation in course of time.

When we compare the entire skeleton of a Jurassic bird with that of a recent one (fig. 23), it strikes us how little specialized the former is, for a bird. The shape of the bones does not as yet reflect the muscular development

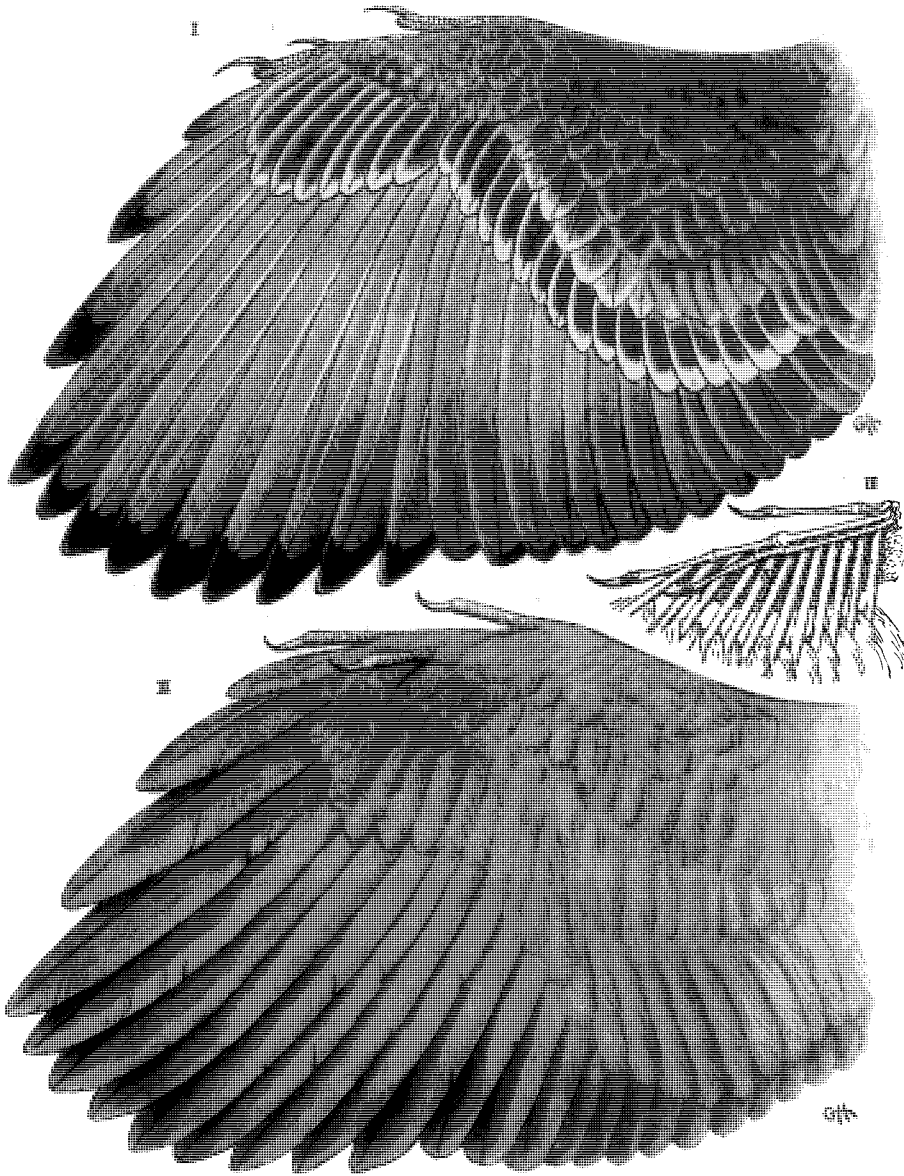


Fig. 22. Wing of *Archaeornis* with expanded primaries and secondaries, I dorsal, II ventral view.
 III Right hand of *Archaeornis*, ventral view, with the barrels in their supposed position.

produced by the constant use of the wings as air-propellers. We have already compared the fore-limbs (fig. 17), but one has only to look at the bones surrounding the organs of the body, and the difference becomes striking. There is an almost box-like compactness about the pigeon, with the pelvis forming the lid, the breast-bone the bottom, and the broad ribs with overlapping

uncinate processes the sides. Of this we find nothing at all in *Archaeornis*, the bony framework of which is weak and delicate as a protective sheath for the soft organs and also for the attachment of the muscles. *Archaeornis* is provided with ventral ribs, into the bargain, but they are only a relic of no use to the bird, and do not strengthen the chest.

We may now stop talking about "the missing link" between birds and reptiles. So much so is *Archaeornis* this link that we may term it a warm-blooded reptile disguised as a bird.

The reconstruction of the outer appearance of an animal from the remote past is of great value for understanding it, hence an important problem for Paleobiology; for this appearance cannot be complete unless we reconstruct the animal in a natural attitude, conforming with its habits or mode of living. Many of the fossil animals were so removed in shape and habits from modern ones that their reconstruction is extremely difficult. In all probability, therefore, the first attempt will prove unsuccessful, but even if it should fail, it may give rise to improvements on the part of other scientists, so that the ultimate result may be salutary.

As *Archaeornis* shows but little resemblance to a modern bird, while being of the utmost importance to our search for the origin of birds, I should very much like to give my readers an idea of its life and habits, and also its phase of development in relation to the rest of the Jurassic fauna. A dry enumeration of the species contemporary with *Archaeornis* would contribute but little to this end. I shall therefore try to give a verbal sketch of the plants and animals among which this unique creature lived.

In the following pen-picture, the only forms mentioned are those well known in Paleontology, the whole organization of which we are thus able to reconstruct; hence it is no fairy-tale with which I wish to entertain my readers. The description of their coloration is of course only guesswork, but nevertheless based on that of creatures now living under nearly similar conditions.

Let us imagine ourselves standing on one of the large islands in the Jurassic sea. A warm and humid breeze fans our faces; we look out over a deep-blue sea replenished with other islands, reaching to the far-off horizon. At some distance from the shore the waves are breaking on the coral reef, on which some large sea-lizards are basking in the sunshine.

The tide is now on the ebb: let us watch them a little closer. During our walk, the varied and beautiful sea-shells lying in the shallow water catch our eye, and we stop to inspect some others, whose flat spirally twisted forms, many of which as large as a plate, sparkle with the fierce splendour of the tropical sun. These Ammonite-shells are now empty and lie on the beach rotting by the agencies of the sun and the wind. The spiral curves of some are enriched with numerous flutings, others are studded, or plain, and the tint of colours on the inside of the broken shells sparkles with the iridescent lustre of the mother-of-pearls.

The large saurians lie fast asleep on the lee side, protected from the spray of the ceaseless breakers pounding on the reef. They are evidently some

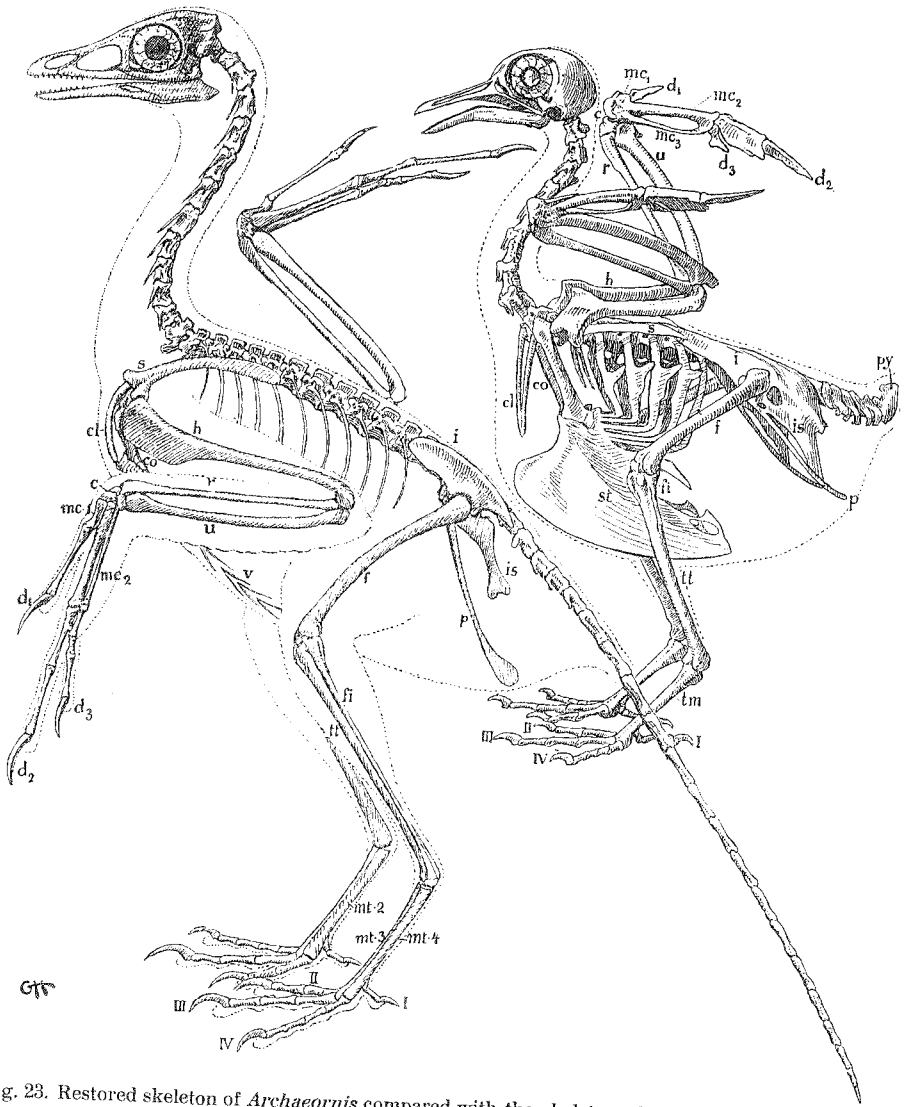


Fig. 23. Restored skeleton of *Archaeornis* compared with the skeleton of a pigeon drawn on a more reduced scale, the birds being of the same size; c carpal, cl clavicle, co coracoid, d digits, f femur, fi fibula, h humerus, i ilium, is ischium, mc metacarpals, mt metatarsals, p pubis, py pygostyle, r radius, s scapula, st sternum, tm tarsometatarsus, tt tibiotarsus, u ulna, v ventral ribs, I—IV toes.

kind of crocodile (*Teleosaurus*), but their life in the sea has somewhat altered their appearance. The dwarfed fore-limbs are strangely peculiar, the arms are short, and the hand diminutive. Just now we see another *Teleosaur* come swimming through the limpid water. It has entered through one of the broad openings in the reef, and as the the water here is smooth, we can watch its every movement. Little of the elongate head with its slender snout is visible above the water, scarcely more than the nostrils and the eyes, placed at the

top of the skull. The small fore-limbs are held close to the body, and it glides forward, propelled by the strokes of its powerful tail. The Teleosaur has now reached the shallow water and waddles clumsily ashore, with ponderous strokes of the tail, heaving itself like a seal upon the level rock. Twice it opens its formidable jaws, showing the powerful dentition with its long and wickedly pointed fangs. Finally it utters a slow hiss of contentment, closing its wily, green-yellowish eyes, and lies down next to the others, wearing the same ineffable and sated crocodilian smile.

Proceeding on our walk we see at some distance another saurian splashing in the shallow water. It has ventured too far in on the flood-tide and has become stranded. It is another sea-crocodile (*Geosaurus*), but of quite a different type from the former ones. The head is also long-beaked and heavily armed, but the skin has no armour; it is smooth and bare. By way of adaptation to its pelagic habits, the limbs have become true paddles, and the long tail ends in a vertical fin. The small deep-set eyes are blood-shot from sheer efforts to get out of the shallow water, which is churned into foam by the violent movements of its tail. But the paddles are not strong enough to drag the heavy body over the sand, and finally it turns over, showing the yellow-white belly shining in the sun.

A couple of long-tailed Pterosaurs (*Rhamphorhynchus*), which were basking on the sandy shore, are startled by the noise and fly with an elegant gliding motion like large swallows over the Geosaur. Their exterior, — the large, elongate head on the short neck, and the tail very long and thin, ending in a rhomboid, leaf-like expansion — presents a most curious appearance. The narrow and tapering wings resemble those of the swifts in shape, but otherwise they differ greatly; the sun shines through the delicate flying-membrane, displaying a row of light specks and rings along the posterior wing-margin. The anterior border, slightly curved, is kept firm and stiff by the long wing-digit.

Almost without any visible movements of the wings, these marvellous reptiles glide to and fro, moving above the water in curves and spirals, now whirling round one another, now floating low near the surface. In a steep curve one of them plunges into the water, presently to reappear with a struggling fish in its beak. Meanwhile the other flying-dragon skims the water-surface with the tip of its lower jaw for small fry and other edible bodies.

At present they are drifting out across the coral reef, straight towards the surf, which is thrown in cascades of foam over the edge of the reef. By an imperceptible turn of the wings, they soar high above the turmoil of the waves, proceeding on their sublime aerial flight across the deep-blue ocean.

While now splashing through the shallow water of the lagoon back to the island, we notice many strange crustacea, whose remains lie scattered around, while the animals crawl away in the water. Some of these have very long tentacles, others seem to be halfway between crawfish and crab. Some most curious sea-urchins lie on the shore; in some, the quills are as delicate as the hairs of a brush, in others they have the shape of figs, oars, or clubs,

and often they are much longer than the body of the animal itself. Of the usual modern forms, we meet but very few.

On land, the soil is covered with small ferns, mosses, and wolf's-claws; there is no grass. The breeze stirs gently the fronds of low, palm-like trees on the neighbouring hills; but they are cycads, not palms. Low scrubs of yew constitute the foreground of the little grove, towards which we wend our way; behind these, numerous tree-ferns rear their delicate crowns. Some distance beyond, some araucaria-like conifers rise above a landscape that looks like a park.

The prospect is not so strange-looking as might be expected, but nevertheless somewhat monotonous, for we do not see a single flower anywhere, nor the swarms of attendant insects. There are, it is true, some wasps and a few clumsy butterflies, but these have no organs for abstracting honey.

The dash of the waves and the roar of the wind are the only sounds reaching our ears; otherwise nature is nearly silent. No clamour of gulls on the shore; the saurians are mute; a faint chirping of locusts is heard.

Some small mouse-like creatures run here and there between the creeping club-mosses; one of them is now busy digging under a small fern, and bending down to watch it a little more closely, we see at once that though it is covered with hair, it is no mouse, its eyes are small and unintelligent. Nor has it the quick and alert motions of the mouse; slowly and steadily it scratches with its fore-paws round the fern-roots. But it is a handsome little creature, olive-brown with irregular yellowish longitudinal stripes, and it is in perfect harmony with its surroundings. Now it has laid bare a root, bites it in two, and commences to devour it.

Taking this little animal in our hand, we find it warm, and cautiously bending aside the hair on the white belly, we see a small slit leading into a cavity, where two diminutive young ones are suspended. They are nearly colourless, and resemble worms rather than young ones of a mammal. From this, however, we learn that it is a very primitive marsupial we have come across. — The mammalian stock was, in the Upper Jurassic, already about five million years old, and yet, during this immense space of time, it had given rise to nothing higher than such puny animals.

With a light and nimble, but somewhat unsteady flight, a gigantic dragon-fly passes by. The expanse of wing seems to be over a foot, and the delicate lace-net of its wings plays in blue and green metallic hues. The silky body and the large eyes glitter in the sun. Restlessly it drifts hither and thither; no sooner has it settled on a twig than it floats away again.

Suddenly a feathered creature launches itself from the top of a tree-fern, sails gently through the air, borne by the expanded wings, and tries to catch the dragon-fly. But this one eludes it by a deft turn, and the bird glides on a little, before it is able to stop. At last it succeeds in turning; it flaps its small wings and tries to rise a little higher in pursuit of its glittering quarry. Its movements look feeble and awkward, evidently requiring considerable effort and prove unavailing. The flight of the dragon-fly is as light and fleeting as

a thought, with ease it baffles the laborious efforts of the bird, and, proficient in the art of flying, it evidently regards the whole pursuit as nothing but an entertaining sport.

After a while, however, it soars into the air, above the tree-tops, leaving the bird to flap down to the roots of a cycad-trunk and rapidly climb to the top. On closer inspection it proves to be a species resembling *Archaeornis*. The wings are partly folded, and it makes use of the claws of the three free digits in holding on to the rough tree-trunk. Though the body is covered with feathers, the aspect of the bare head and neck gives one the impression that the animal is a reptile masquerading in borrowed plumes. As for the head, it seems hardly possible that it belongs to a bird.

We cannot call the foremost part of the toothed jaws a beak, for there is no horny sheath, but they are covered with a thick skin, studded with large scales, as in a lizard's head (fig. 24). The nostrils open anteriorly at the snout, as in a reptile; the iris of the eyes glitter coral-red, and the ear-opening is conspicuous. The bare, rough skin is greyish, and on the neck the feathers are black and white, while the rest of the plumage is plain brown.

The *Archaeornis* has now ascended the trunk and leaps onto the large, pinnate fronds; it perches comfortably on the midrib of one of these, and sets up a series of hoarse cries. After a while, another *Archaeornis* glides through the air and lights next to it. This one is reddish in the naked parts of the head and neck; its plumage is deep steel-coloured and more gaudy. The bird is apparently a male, and starts at once to make advances to the first one. It bends its head quite low, raises the handsome blue feathers of the back, and displays the feathers of the long tail so as to show its entire beauty. After this it carries its head erect and inflates a mighty throat-pouch, which gradually assumes a rich scarlet hue.

The female at first retires a little, but by and by seems fascinated by this display of colour; she bends her neck, giving him the chance of caressing her with his "beak", and both utter some snarling, unmelodious sounds, an expression of mutual satisfaction.

But at the same moment, the idyll comes to an end. A second male lights with a crash and endeavours to grasp the female by the scruff of the neck, as if to take possession of the fair one by force. This puts the first male on his mettle. With raised feathers and mouth open, he hurls himself upon his rival, and they close in mortal combat. They have seized one another with their teeth, and while the feathers are flying in all directions, they dig their long and sharp finger-claws into each other's skin and flesh. Blood flows freely, and, a shapeless lump of feathers, the two opponents fall from the tree onto the ground, where the struggle continues among the ferns.

The courted female, of course, is an interested spectator, looking on from the leaves of the cycad. Now the first of the males, now the second, is on top, each one trying to release himself and give his adversary the coup-de-grâce; they have forgotten everything around them.

Now we catch sight of a graceful little creature, moving with the swiftness

of an arrow, through the open underwood. With the small fore-limbs pressed against its breast, head and fore part stretched forward, and the tail curved upwards, it seems to fly through the air, carried on by the strong hind-limbs. It is *Compsognathus* (fig. 119) in search of prey.

As soon as the little dinosaur beholds the rolling tangle of feathers amongst the ferns, it starts and stops a moment to see what it is. The tangle now resolves into the two males, one of which lies powerless on the ground, while the other stands to his feet and shakes his feathers.

Meanwhile the female in the tree has become aware of the lurking saurian, and gives vent to some shrill cries of warning. But her mate beneath seems to pay no attention; flushed with victory he boasts his pride and raises his head in order to announce his conquest to all the world, when suddenly *Compsognathus* leaps upon him, and the shout of victory ends in a half-smothered cluck.

After having dispatched the bird, the little dinosaur settles down on its hind-legs, but not quite as a kangaroo. It is delicate and elegant in build, with horny granular scales, which on the back become somewhat larger and fuse together so as to form a well-defined longitudinal ridge. The feet are very much like those of a bird, and the three fingers of either fore-limb hold on to its prey, upon which it is feasting.

The female in the cycad persists in chiding the impudent murderer, — and the curtain drops.

The animals here depicted give of course only a vague idea of the abundant fauna of the Jurassic era, but the reader may possibly form some conception as to the stage of evolution at which the animal world at this period had arrived.

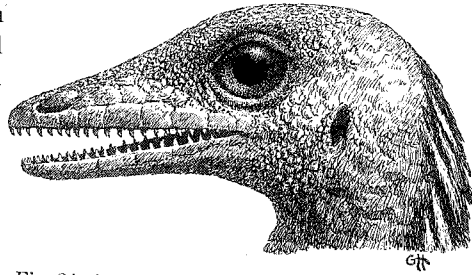


Fig. 24. Supposed exterior of the head of *Archaeornis*, nat. size.

ICHTHYORNIS AND HESPERORNIS

The next fossil bird, of importance to our researches, is *Ichthyornis* of the Cretaceous period, described by Marsh (10).

The most interesting part of the skull of this creature is the lower jaw (fig. 25), which is well preserved. "The two rami are entirely separate, having been united in front only by cartilage". This is a reptilian feature, and so is the fact that the teeth are implanted in distinct sockets. "They are all sharp and pointed, more or less compressed, and strongly recurved. The crowns are coated with enamel, and the two fore and aft cutting edges are sharp and smooth, without serration". "The dental succession took place vertically, as in Crocodiles and Dinosaurs". "The dentigerous portion of the lower jaw is so similar to that of some of the smaller Mosasauroid Reptiles, that, without other portions of the skeleton, the two could hardly be distinguished" (Marsh 10).

"The brain of *Ichthyornis* was remarkably small, and, in its main features, strongly reptilian" (fig. 88). "The most noticeable reptilian features are the elongated form, and prominent optic lobes". "In comparing the brain-cavity of *Ichthyornis* with that of *Sterna* (fig. 26), the strong contrast in size is at once apparent, while the most marked difference is seen in the cerebral hemispheres". "The bulk of the entire brain of *Ichthyornis* would be less than one-third the size of that of the Tern".

"While all existing birds have the peculiar saddle-shaped vertebræ, those of *Ichthyornis*, and its near ally *Apatornis*, are biconcave (fig. 27). This form is seen in a few recent and in many extinct Reptiles, and in the Amphibians; but it is especially characteristic of Fishes, from which class it was undoubtedly inherited by the superior group" (10).

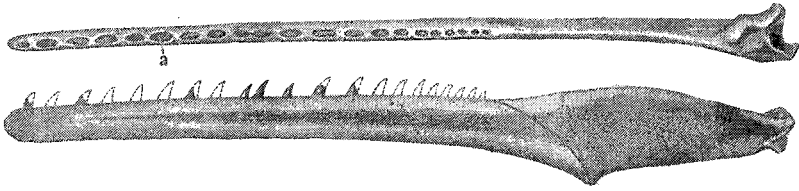


Fig. 25. Mandible of *Ichthyornis dispar*, upper and outer view, somewhat enlarged, after Marsh; a tooth-groove (alveola).

The pelvis (fig. 10, D) is small in comparison with the pectoral arch, and the ischium is not joined to the ilium posteriorly. The bones of the wings and feet are like those of recent birds.

Another bird from the Cretaceous period was by Marsh named *Hesperornis regalis*, i. e. "the royal bird of the west". Its size, too, was considerable; "the skeleton, if extended, would measure about six feet (1.8 m) from the point of the bill to the end of the toes" (10). Nevertheless the word "royal" is somewhat misleading. As will appear from the following pages, the bird was a Loon and unable to stand erect.

The skull is shown in figs. 28, 29, and 30. It is long and narrow, closely resembling the skull of the Great Northern Diver, *Colymbus glacialis*. While Marsh (10) also states this in general, yet he thinks that "in its more important character, the skull of *Hesperornis* resembles that of the *Ratitæ*, or Struthious birds".

This is by no means correct, and with reference to this question, it will be sufficient to quote R. W. Shufeldt (14), who has compared the forms mentioned, and says as follows: "it will once and for all disabuse the mind of the paleontologist with respect to there being any agreement of characters, when we come to compare the skull of the ostrich with that part of the skeleton of *Hesperornis*". "Indeed, no two birds' skulls, either of existing or extinct species, could be more unlike each other than are the skulls of an *Hesperornis* and an Ostrich".

On comparing the individual bones of the skulls of *Colymbus* and *Hesperornis* in fig. 28, we soon discover that their close resemblance is due to real

Fig. 26. Outline of the skull and brain-cavity of *Ichthyornis victor* (to the left) and of *Sterna cantiaca* (to the right); seen from above; ol olfactory lobes, c cerebral hemispheres, op optic lobes, cb cerebellum; after Marsh.

affinity, and although there is a difference of millions of years in the ages of the two birds, they are more closely related to each other than are *Colymbus* and the wild Goose (*Anser ferus*, see fig. 3), which are contemporaneous.

It is, therefore, much easier to enumerate the differences than the resemblances. *Hesperornis* has teeth in its jaws, a smaller braincase, the pterygoid has a different form and position from that in *Colymbus*, and the splenial is conspicuous on the outside of the mandible — all very important features.

"The teeth of *Hesperornis* are true teeth, with their distinctive characters as well marked as those of any reptile. In the upper jaw, they are confined to the maxillary bone alone, the premaxillary being entirely edentulous. In the lower jaw, the teeth extend from very near the anterior extremity of the ramus along the entire upper border of the dentary bone". "The teeth were implanted in a continuous groove, somewhat like those of *Ichthyosaurus*. From the sides of the groove slight projections extend between the teeth". "There were fourteen functional teeth in the maxillary bone, and thirty-three in the corresponding ramus of the lower jaw". So in all, the bird had no less than 94 teeth.

"The teeth of *Hesperornis* were gradually replaced by successional teeth, and this took place in a manner very similar to that in some reptiles. The germ of the young tooth was formed in the inner side of the fang of the tooth in use" (fig. 28, 3). "In form of crown and base they closely resemble the teeth of Mosasauroid reptiles" (fig. 28, 4). "The outer and inner surfaces of the crown are separated by sharp ridges, which are without serrations". "In all their main features, the teeth of *Hesperornis* are essentially reptilian, and no anatomist would hesitate to refer them to that class, had they been found alone" (10).

Only the posterior part of the pterygoid bone is preserved and, not resembling that of any other known bird, is of course somewhat difficult to understand. This I was therefore not able to do, before I had made a plastic model of the pterygoid and of the whole skull from the drawings by Marsh. Not till then did I understand that the bone could not be placed in relation to the quadrate and basisphenoid otherwise

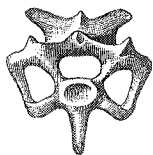
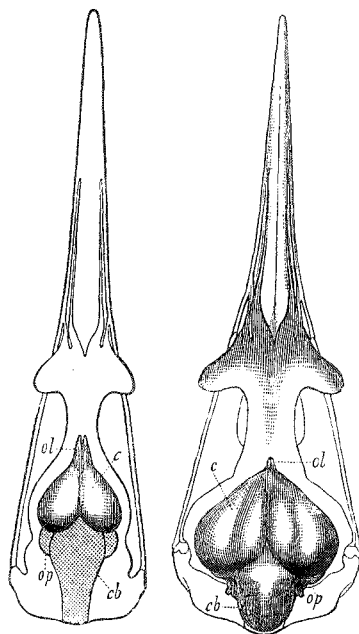


Fig. 27. Twelfth cervical vertebra of *Ichthyornis dispar*, front view; twice natural size; after Marsh.

than I have shown it in fig. 29, 1. Marsh remarks that facets (fig. 29, 4, f), situated near the posterior end of the pterygoid articulate with strong basi- pterygoid processes (seen in fig. 29, 1, on both sides of the letters Bsh, and in fig. 31, 1, Pb), arising from the body of the basisphenoid, and not from the rostrum. There is also a small process (fig. 29, pq) for articulation with

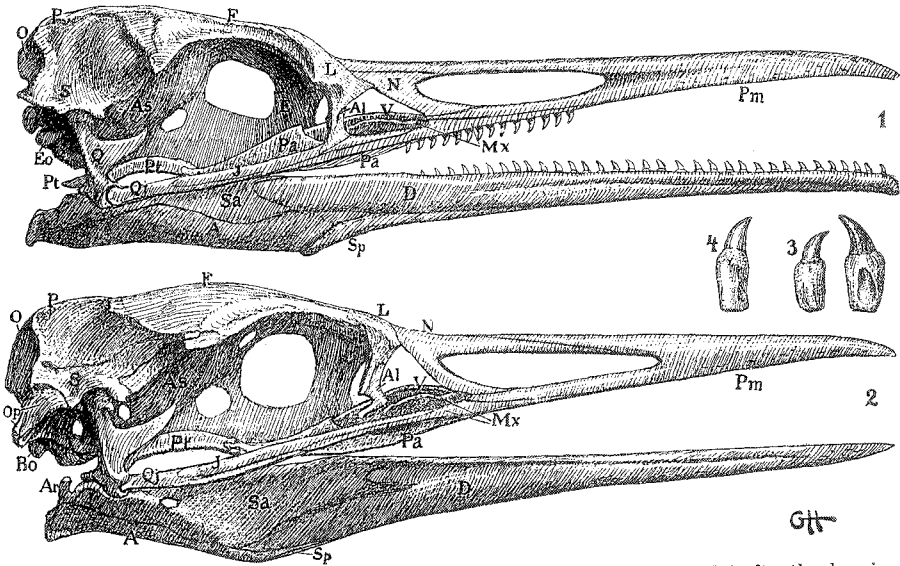


Fig. 28. Skull and mandible of 1 *Hesperornis regalis*, drawn from a plastic model after the drawings of Marsh, 2 Great Northern Diver (*Colymbus glacialis*); 3 two teeth of *Hesperornis regalis*, enlarged, 4 tooth of Mosasaur, after Marsh; the lettering as in fig. 3, Al adlachrymal, Sp splenial.

the quadrate. The anterior part of the pterygoid, which I have drawn with a dotted outline in fig. 29, 3 and 4, is not preserved and of course hypothetical.

This strange pterygoid is strongly reptilian. I have drawn the skulls, seen from behind, in fig. 31 to show this. In general the pterygoid in a bird's skull cannot be seen from behind (fig. 31, 2), but in some lower forms, for instance the Divers (fig. 31, 3), we observe how it articulates with the quadrate, just where the shaft of this bone descends at the distal extremity, which forms the articular surface for the mandible. In *Hesperornis* this articulation is nearly in the same place, but behind this the pterygoid has a leaf-shaped prominence (fig. 29, 1, 3 and 4) extending backwards and resting on the posterior part of the distal extremity of the quadrate (fig. 31, 1). This is also distinguishable in fig. 28, 1.

Exactly the same feature is characteristic of the reptilian skull (fig. 31), and the basiptyergoid processes we also find there. In *Hesperornis* it is, therefore, an inheritance from a reptilian ancestor.

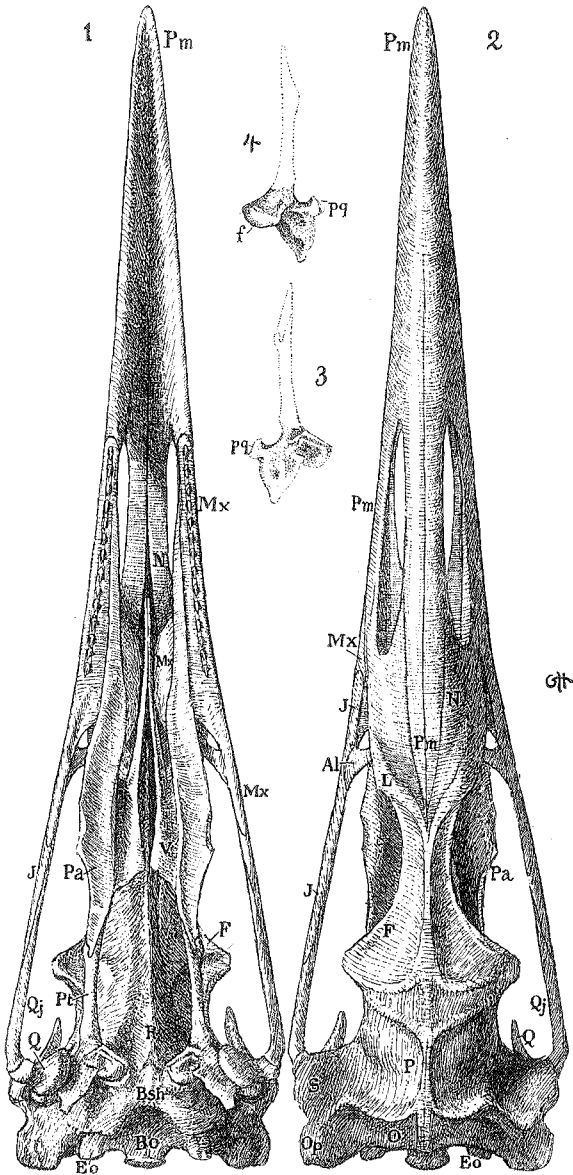
In the skull of a young bird, the occipital condyle may be seen to be composed of elements from both the exoccipitals and the basioccipital (fig. 31, 2 and 3). This, too, is reminiscent of a reptile. R. S. Lull says that in *Anchisaurus*

Fig. 29. Skull of *Hesperornis regalis*, drawn from plastic model, 1 ventral, 2 dorsal view; 3 and 4 the pterygoid of same, 3 in ventral, 4 in dorsal view. Lettering as before; f facet articulating with basiptyergoid process, pq process articulating with the quadrate.

(15): "The occipital condyle is composed of a median basioccipital element and a lesser lateral portion from each of the exoccipitals". And Nopcsa says that the same thing holds true of *Compsognathus longipes* (16): On the kidney-shaped occipital condyle is distinctly seen "wie an seinen äusseren Ecken die Exoccipitalia einen nicht unbedeutenden Anteil nehmen". In a young specimen of *Hesperornis* we should no doubt find the same.

Fig. 31 also shows us how very disproportionate the braincase of *Hesperornis* was to that of a recent bird. The hindmost parts of the skulls in Nos. 1 and 3 are nearly the same, but in *Colymbus* the braincase rises considerably above these, while in *Hesperornis* we see the tips of the postfrontal processes only.

The brain, consequently, was very small and wholly reptilian in type. In fig. 30 we can compare it with that of an Alligator, and of a Loon. The olfactory lobes were large and elongate, the cerebral hemispheres much smaller than in any existing bird, and strongly resembling the corresponding parts in reptiles. The similarity in size and position of the optic lobes to those in the Alligator is especially noteworthy. We shall return to this brain in Part III, making a comparison of brains in birds and reptiles (see fig. 88).



Before leaving the skull, I should like to call attention to the lachrymal, which articulates with the jugal, thus in all probability being a compound bone, including the adlachrymal in its lower part (see fig. 5). In the lachrymal of *Colymbus*, a suture may be traced (fig. 28, 2), which indicates that an adlachrymal is present, and this entitles us to infer that the same bone is present also in *Hesperornis*.

Along the roof of the orbits there are well marked glandular depressions both in *Colymbus* and *Hesperornis*, especially indicative of their aquatic habits. I think that the outer half of the depression is wanting in *Hesperornis*, because this border of the frontal bone is easily broken off, and was lost in three of the skulls from which I have drawn fig. 28, 2. Along the bottom of the depression is an extended row of small holes (distinctly visible in fig. 30, C), which makes the bone fragile along this line, and I think the same is the case in *Hesperornis*.

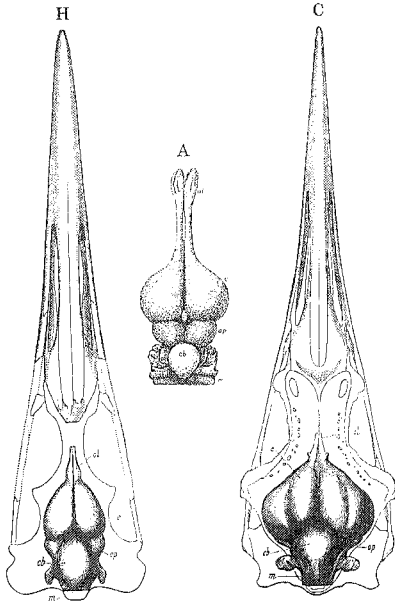


Fig. 30. Outline of skull and brain-cavity of H *Hesperornis regalis*, C Great Northern Diver (*Colymbus glacialis*), both seen from above, after Marsh; A Brain of Alligator, seen from above; c cerebral hemispheres, cb cerebellum, m medulla, ol olfactory lobes, op optic lobes.

Now we pass on to the discussion of one of the most characteristic portions of the skeleton: the mandible. That of *Hesperornis* would fit a reptile much better than a recent bird. In fig. 28 we have already had occasion to compare the outside of it with that of *Colymbus*, but in fig. 32 we see this mandible isolated, both in outer and inner view, compared with those of birds and of reptiles. To an untrained eye it might look as if Nos. 3 and 9 belonged to some sort of reptile, while No. 11 undoubtedly was that of a bird. But quite the opposite is the case.

In order to see the individual bones of the lower jaw in their most primitive relationships, I have drawn those of *Eryops*, a stegocephalian from the Permian of Texas, in Nos. 1 and 2. For our particular purpose we need only notice the following components: angular, articular, surangular, prearticular, coronoid, dentary, and splenial. In the illustration, we can trace the individual bones throughout the various forms of reptiles right on to the birds, and see how very similar their position is. On the whole, they are almost identical.

The bone that most strikingly demonstrates inheritance from the reptiles, is the splenial. In these it is discernible both on the outside and the inside of the lower jaw, forming a part of the inferior border. Exactly the same thing is found in *Hesperornis*, but in all recent birds it has vanished from the outside of the mandible. In their case it just reaches the lower edge, but

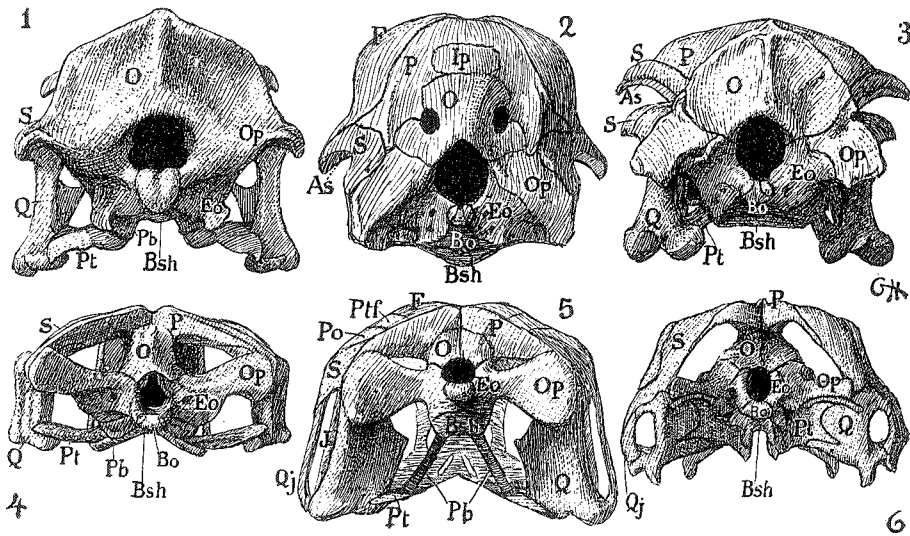


Fig. 31. Skull seen from behind of 1 *Hesperornis regalis*, drawn from plastic model, 2 Wild Gosling (*Anser ferus*), 3 Great Northern Diver (*Colymbus glacialis*), 4 *Varanus* after Zittel, 5 *Scaphognathus Purdoni*, a Pterosaur from the Upper Jurassic, after E. T Newton, 6 *Tuatera* (*Sphenodon*), after Zittel. Lettering as before; Pb basiptyergoid process.

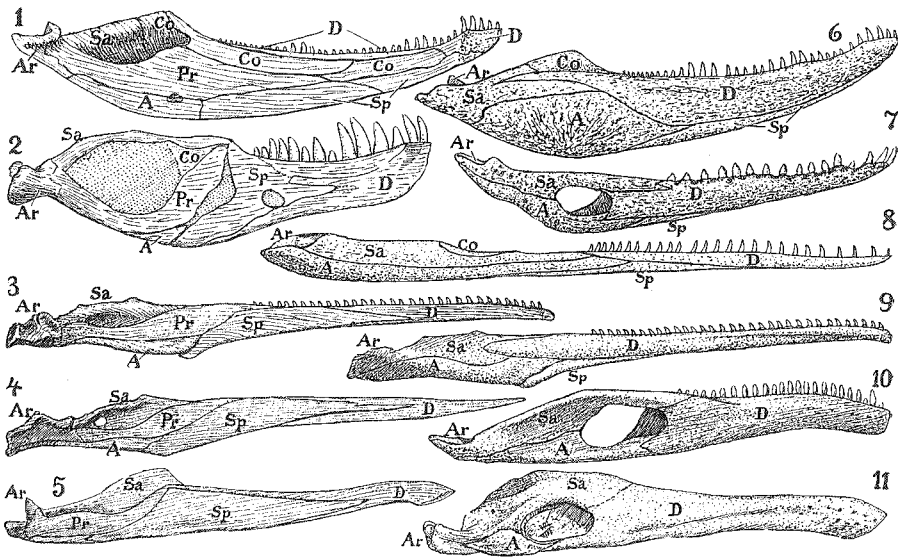


Fig. 32. Mandibles, 1—5 from the inside, 6—11 from the outside. 1 and 6 *Eryops megacephalus*, a Stegocephalian from the Permian, after R. Broom, 2 *Tyrannosaurus rex* from the Upper Cretaceous, after H. F. Osborn, 3 and 9 *Hesperornis regalis* after Marsh, 4 Great Northern Diver (*Colymbus glacialis*), 5 Gosling (*Anser ferus*), 7 Young Crocodile, 8 *Geosaurus suevicus* from the Jurassic, after E. Fraas, 10 *Plateosaurus longiceps* from the Upper Triassic, after O. Jaekel, 11 *Struthiomimus altus* from the Cretaceous, after H. F. Osborn. A angular, Ar articular, Co coronoid, D dentary, Pr prearticular, Sa surangular, Sp splenial.

extends no further, only in *Colymbus* can we catch a mere glimpse of it from the outside, not so distinctly as I have drawn it in fig. 28, 2. In many Dinosaurs, too, the splenial has disappeared from the exterior aspect of the mandible (fig. 32, 10 and 11). In birds, the coronoid has vanished.

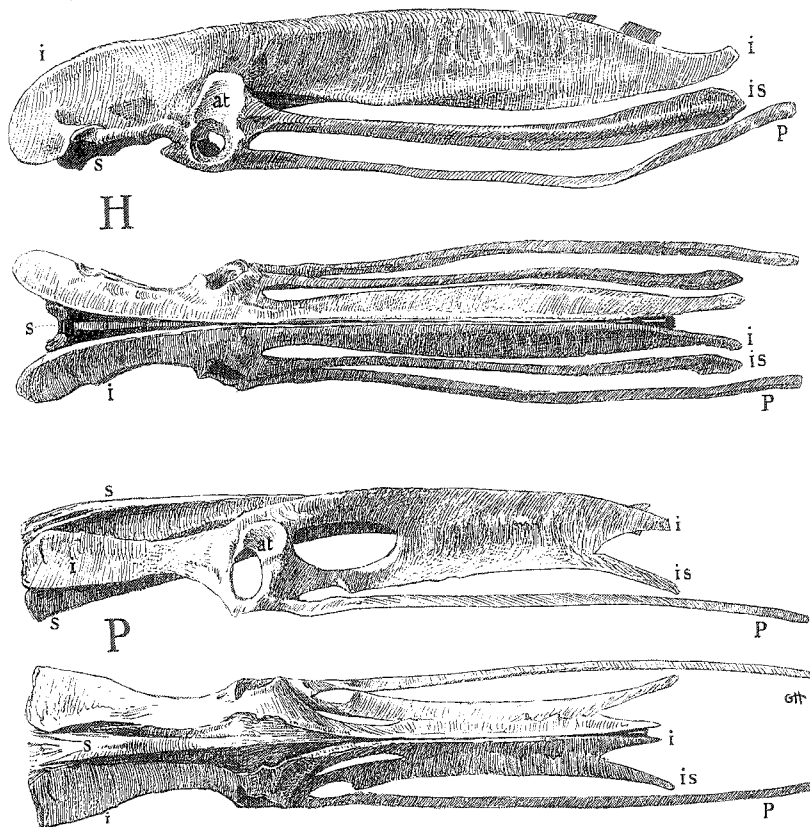


Fig. 33. Pelvis, lateral and dorsal view of H *Hesperornis regalis*, after Marsh, P Great Crested Grebe (*Podiceps cristatus*); at antitrochanter, i ilium, is ischium, p pubis, s sacrum.

"As the lower jaws of *Hesperornis* were united in front only by cartilage, as in Serpents, and had on each side a joint which admitted of some motion, the power of swallowing was doubtless equal to almost any emergency" (10).

The vertebræ resemble the corresponding elements in *Colymbus glacialis*, and were saddle-shaped. The shoulder girdle (fig. 8, 4) supported only a degenerate limb, the relic of a wing, the forearm and hand being lost. The clavicles were separate, not coalesced so as to form a furcula.

The uncinæ processes (fig. 66, 4) had not yet fused with the ribs, as in recent birds.

The pelvis (fig. 33 H) has a considerable resemblance to that of *Podiceps* (fig. 33 P), but its primitive character is indicated by the distally disunited ilia and ischia. "The acetabulum differs from that in all known birds, in being

closed internally by bone, except a foramen that perforates the inner wall, as in the Crocodiles" (10). Above the acetabulum there is a large anti-trochanter (fig. 33, at), or articular surface for the trochanter of the femur, which is extremely short and stout bearing a striking resemblance to the femur of *Colymbus septentrionalis* (fig. 34 H and C).

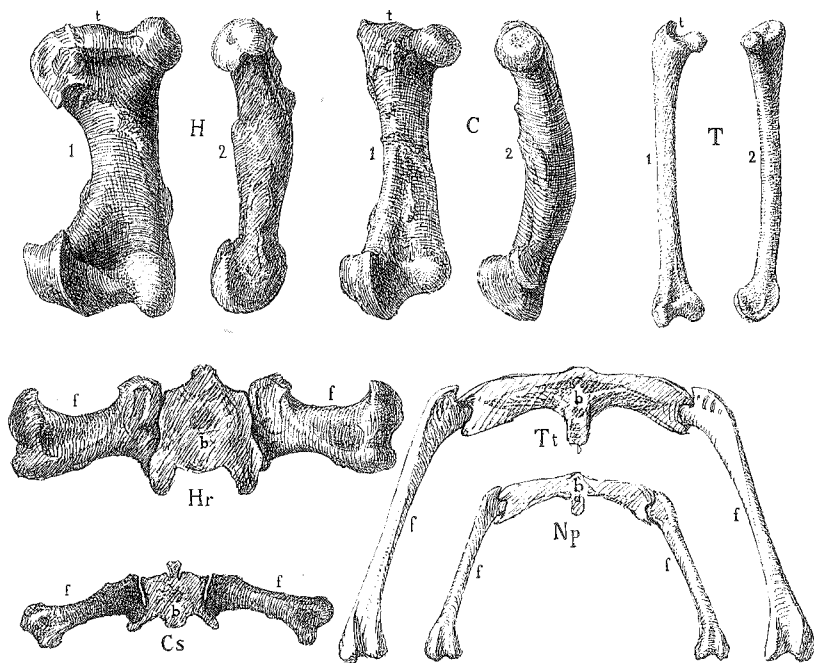


Fig. 34. Left femur of H *Hesperornis regalis*, after Marsh, C Red-throated Diver (*Colymbus septentrionalis*), T Black Grouse (*Tetrao tetrix*), 1 inferior, or posterior, view, 2 inside of femur. The other four drawings show the relationship of the femur to the pelvis in Hr *Hesperornis*, Cs *Colymbus*, Tt *Tetrao* and Np Wimbrel (*Numenius phaeopus*), all viewed from before; b pelvis, f femur, t trochanter.

The articular surface of the trochanter is large and lies lower than the head, still lower than that of the Loon. This feature is important for understanding the position of the hind-limbs, because the femur, when the articular surface of the trochanter plays against the antitrochanter of the ilium, will move almost in the horizontal plane of the pelvis (fig. 34, Hr and Cs), while in the fowls these planes meet at a considerable angle (fig. 34 Tt and Np). The femur of both *Hesperornis* and *Colymbus* is furthermore somewhat curved, with the convexity forward, and both have nearly the same strong prominences for the attachment of muscles. Likewise in the distal end of the bone characteristic resemblances between the two birds are to be found. The tibiotarsus and the fibula remind one very much of those in *Colymbus*, yet the two bones were not fused together but united by cartilage.

A special feature in several diving birds is the development of the patella,

this bone having fused with a prominence of the tibiotarsus, the cnemial process, and in *Colymbus* especially it forms a considerable projection from the proximal end in the longitudinal axis of the bone. In *Hesperornis* the patella has attained similar dimensions, but it is not coalesced with the tibiotarsus (fig. 35); it is perforated by a large foramen for the tendon of the

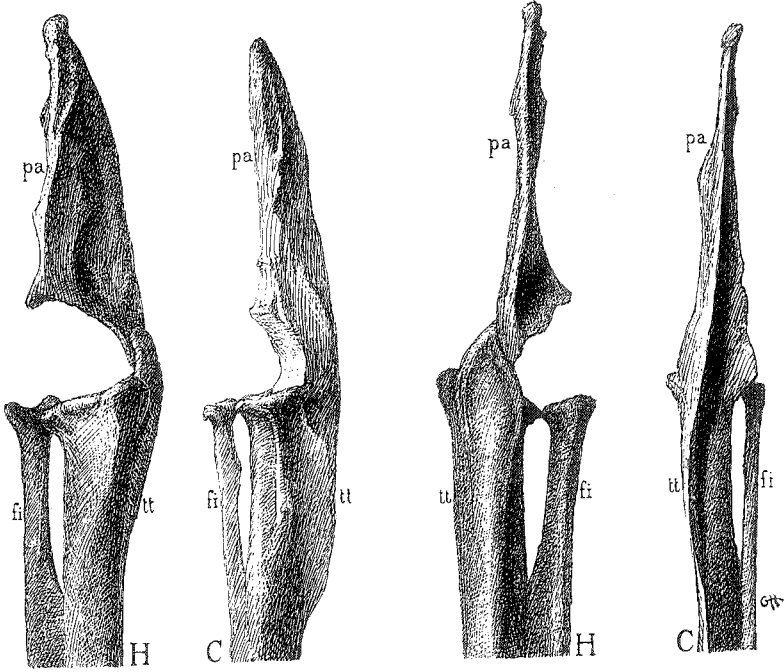


Fig. 35. Left knee-joint H of *Hesperornis regalis* and C of Great Northern Diver (*Colymbus glacialis*). seen in two different views; H drawn from plastic model after details in Marsh's drawings; fi fibula, pa patella, tt tibiotarsus.

ambiens muscle, agreeing in this respect with the patella of the Cormorants (fig. 36).

In passing over the patella, the tendon of the ambiens muscle has, in several aquatic birds, excavated a groove in the bone (fig. 36, 1), and in some cases this groove has become a hole, through which the tendon glides (fig. 36, 2). R. W. Shufeldt (17) has called attention to the fact that the patella in the Cormorant is a compound bone, formed by coössification of the true patella to a part of the cnemial process, loosened from the tibiotarsus. In fig. 36, 5 we notice that the patella is composed of two pieces, and in a newly hatched young one, the two centres of ossification are still separate (fig. 36, 6); in all probability, the same condition prevailed in the adult *Hesperornis*. The powerful cnemial process in *Colymbus* (fig. 35, C, pa) is doubtless also formed by coössification with the patella; the small bone in the tendon of musculus extensor femoris, which some authors supposed to be the patella, has later proved to be one of the sesamoid-bones, frequently occurring in the knee-joint.

As will appear from fig. 38, the fourth toe of *Hesperornis* is very strong and powerful in proportion to the other three, and has formed a broad articulation with the tarsometatarsus; the third toe is relatively the weakest. As the fourth toe is the longest, the foot is not unlike that of the Cormorant, and the weak third toe does not suggest that the bird had lobate toes; most likely the foot was wholly webbed.

Having thus called attention to the striking points of resemblance, throughout the entire skeleton, between *Hesperornis* and *Colymbus*, we entertain no doubt as to their close affinity. But Marsh came to a different conclusion; he writes as follows: "The Struthious characters, seen in *Hesperornis*, should probably be regarded as evidence of real affinity, and in this case

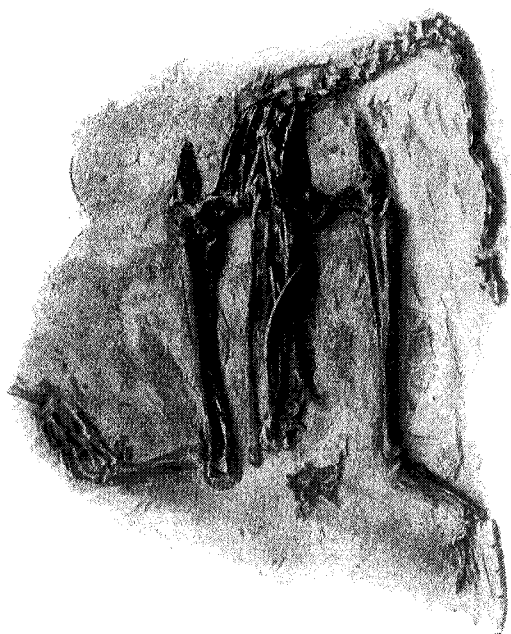


Fig. 37. Skeleton of *Hesperornis regalis*, lying on its back in the position in which it was found by C. H. Sternberg; the head is missing.

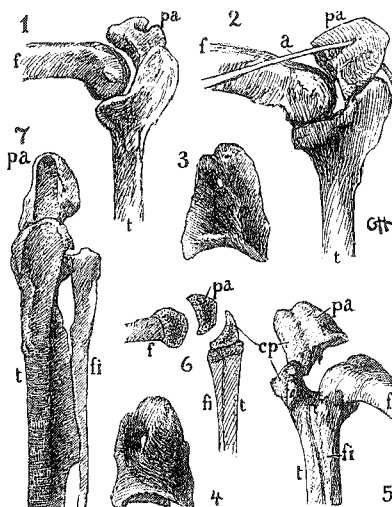


Fig. 36. Patella and the adjacent bones in 1 Red-breasted Merganser, *Mergus serrator*, 2—7 different species of Cormorants: 2 *Phalacrocorax carbo*, 3 and 4 *Nannopterum harrisi* (front and back of patella), 5 *Ph. auritus*, 6 newly hatched young one of *Ph. atriceps*, 7 *Ph. urile*; 3—7 after R. W. Shufeldt; a tendon of the ambiens muscle, cp cnemial process, f femur, fi fibula, pa patella, t tibia.

Hesperornis would be essentially a carnivorous, swimming Ostrich".

When writing the preceding pages about *Hesperornis* in 1912, I did not know of a very interesting paper by D'Arcy W. Thompson (18) on the same subject. After having compared the skeletons of the two birds, bone for bone, he recapitulates no less than 25 different points in which the close resemblances in *Hesperornis* and *Colymbus* differ from the Ratites. We quote as follows: "To sum up, it appears to me that from purely osteological characters, the wide difference between *Hesperornis* and

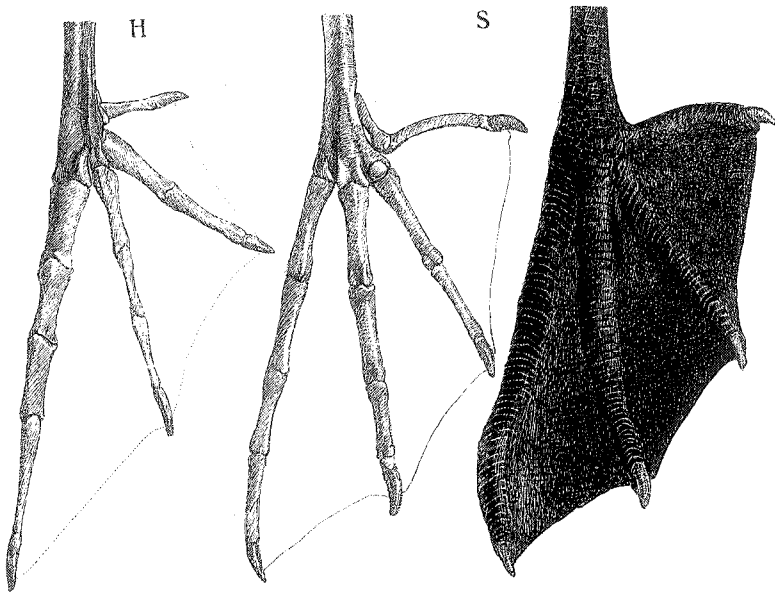


Fig. 38. H Right foot of *Hesperornis*, the dotted line indicating the outline of a supposed web; greatly reduced; S right foot of *Cormorant*, *Phalacrocorax carbo*.

any Ratite, and its close resemblance to *Colymbus* or to *Podiceps* is clear and patent”.

Every true naturalist will agree with D’Arcy W. Thompson and consider his conclusion final, but this “swimming Ostrich” still seems to haunt the brains of scientists, and has assumed strange forms in modern text-books. Thus in “Die Wirbeltiere” (Berlin 1911) p. 174, Otto Jaekel mentions the *Hesperornes* as shore-runners, “die sich offenbar nicht der Schwimmbewegung angepasst hatten, sondern nur als Laufvögel am Ufer lebten”. This is indeed the most preposterous misjudgment of the prominent characters of *Hesperornis*.

Marsh has drawn his restoration of the skeleton in a position which the bird was quite unable to sustain. The femora are directed forward, and the trochanter thereby separated from the antitrochanter in an unnatural way. In fig. 37 we see the hind-limbs of *Hesperornis* in their natural position in rela-

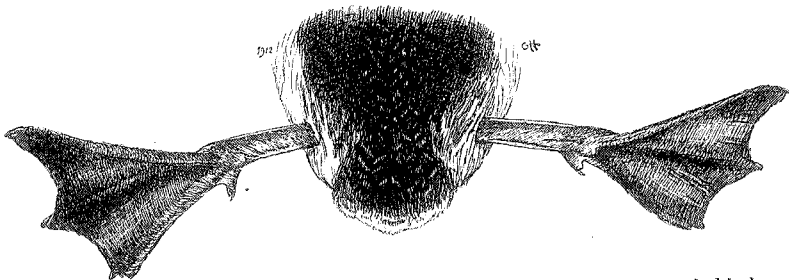


Fig. 39. Hind part of Red-throated Diver, *Colymbus septentrionalis*, seen from behind and from above, the feet being moved backward during swimming.

tion to the pelvis. The skeleton of a *Colymbus* would present quite the same figure.

Now let us see how a Diver swims. A mere glance will suffice to show that the hind-limbs are used as a pair of level oars, directed to either side of the body, and not moving underneath, as is the case in Ducks for instance. The feet present great resistance to the water when moved backwards (fig. 39), while by forward-motion the greatly compressed tarsometatarsus cuts the water like a knife.

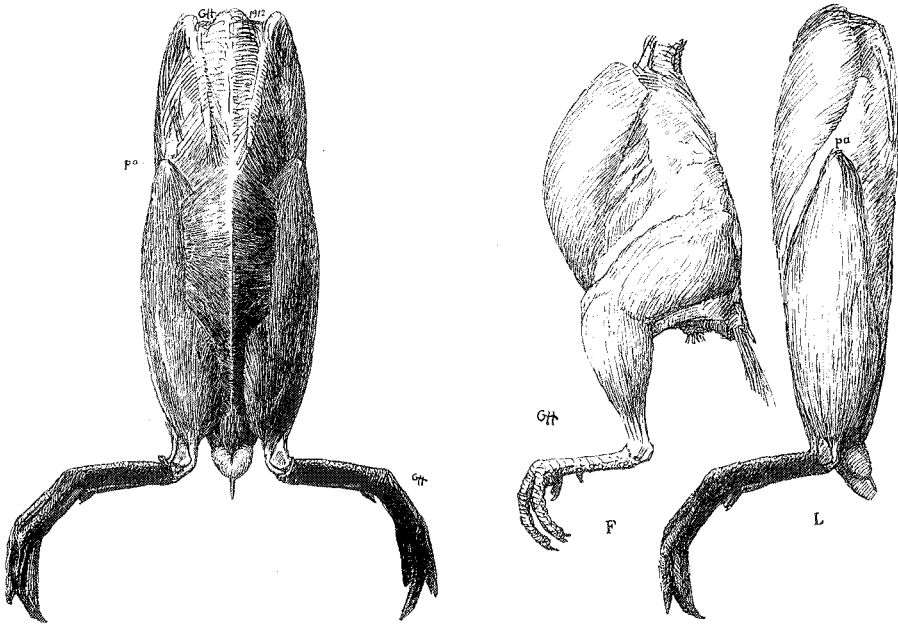


Fig. 40. Skinned body of a Loon in dorsal view; the fore-limbs cut away; pa the tip of patella.
Fig. 41. Skinned body of F. Pheasant and L Loon, lateral view.

Why does a Diver keep its feet in such a position? When we remove the skin and lay bare the muscles, the cause becomes evident at once (fig. 40), — the bird cannot do otherwise. In figs. 41 and 42, I have drawn the skinned body of a Pheasant, a typical walking and running bird, beside that of a Diver. A comparison will show why the Diver can move on land with the greatest difficulty only, the thighs and shin-bones being closely tied to the body by muscles and fibrous tissues, thus limiting the means of locomotion to that of swimming. In the game-birds, on the other hand, the entire hind-limb moves easily; hence, they are able to walk and run, but not to swim and dive.

Fig. 43, L shows that the strong patella and cnemial process in the Diver is used for attachment (origin) of large muscular bundles, mainly from the gastrocnemius externus and internus, and that the individual bundles of these are united, just above the heel, to the strong tendon, inserted at the back of

the proximal part of the tarsometatarsus. It is the extensor of the foot, and the bird is capable of moving it backwards with great force, when bending at the heel. Hence, it is the main propelling muscle in swimming. A comparison with the gastrocnemius of the Pheasant (fig. 43, F) is instructive. The Diver seems to have developed its large patella and cnemial process because its femur, through the efforts of the body to assume the form of a torpedo, had to become shorter and shorter, so that there was not room enough for the attachment of the gastrocnemius. In the skinned body of the Diver, the femur is not visible, as in the Pheasant, only the uppermost tip of the patella being discernible (figs. 40 and 41, pa).

From this explanation we learn to what extent the skeleton is stamped by the special habits of the bird, and as the skeleton of *Hesperornis* in the region of the pelvis and hind-limbs bears the most striking resemblances to that of *Colymbus*, we may take it for granted that the muscles, too, were not essentially different. *Hesperornis*, therefore, was obliged to move in the same manner; it was not able to walk, much less to run on the shore, as O. Jaekel surmises, in fact, no more than the Diver is able to do so, for in that case its toes would also have been shorter.

Having thus shown how the skeleton of *Hesperornis* clearly demonstrates its habits and mode of locomotion, we have no great difficulty in imagining the life of this bird in the remote Cretaceous era, millions of years ago, when the pinnacles of the Rocky Mountains, forming islands of different dimensions, rose above the surface of the extensive ocean.

It is before dawn and quite dark as yet. The tempest of the night has subsided, but large breakers are constantly rolling towards the shore. The water rushes between rocks and islets, forming eddies in the narrows, and rises, foaming through cavities, gushing out and spouting high into the air, like a series of fountains, splashing out upon the stones and swirling down along the cracks and crannies.

Then follow the back-wash of the waves; hollow and gurgling sounds re-echo from the surrounding ravines, as the water recedes, — a crash of bursting bubbles in rapid succession, a boom of spouting, splashing, and seething torrents in cascades from rocky ledgers, and — the swell rises once more.

A fleeting phosphorescence seems to dart across the rising swell. As if leaping out from the deep, it spreads with the speed of lightning, blazes on the crests of the waves and vanishes in the wide vales of the surge. Silvern streaks glitter amongst gleams of emerald-green, while glints of amethyst-blue, like shooting stars, start up from the dim sea-bed.

Suddenly all has become calm, and it is as dark as before. Then the whole symphony of sounds from the rising and falling surge again strikes the ear. Now it glitters once more farther out at sea — the ghostly flames seem to play hide-and-seek, chasing one another across the turbulent waves.

A long, gloomy shadow glides forward in their midst, while the movement brings sparkling life to fresh millions of luminous micro-organisms. The colours, tumbling headlong in endless confusion, are reflected by the wet

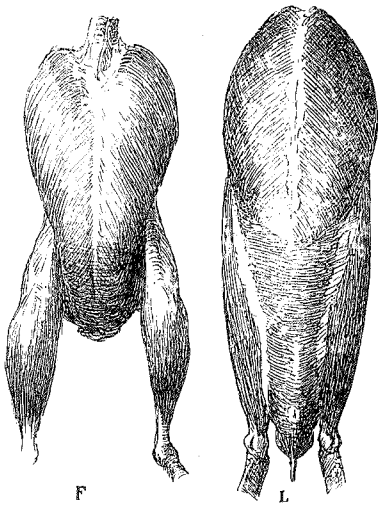


Fig. 42. Skinned body of F. Pheasant and L. Loon, ventral view.

snake-like body of a Mosasaur (*Clidastes*), the peculiar head of which rises above a wave-crest. The teeth glitter in the long mouth of the saurian as, without a sound, it winds its way through the floating streams of fire. The spectacle is fraught with wondrous beauty, and with horror. But now we are startled by the sound of a shrill scream.

A wailing howl succeeds, and a foreboding sound as if heavy bodies were being dragged across the stones. Still more dreadful, the shriek is heard once more, it is repeated again and again, is re-echoed, now far-off, now close by, punctuated by angry mewling sounds every now and then. With a splash from its hind-paddles and a stroke of its long tail-fin, the Mosasaur has vanished from the scene.

The nocturnal fireworks of the sea have disappeared, but the screams are still heard; they rise and fall like the waves of the ocean; — it seems as if all the imps of hell have met on these desolate rocks. We turn our eyes to the east and observe that the horizon is silhouetted against a faint, cold, grey glimmer in the sky. It is but the harbinger of day, and yet, the jarring notes of unremitting sounds are shouts of joy, greeting the dawning day.

Presently the morning twilight emerges from the bosom of the ocean. The eastern sky clothes itself in a yellowish hue; the pale light gives form to wave-worn rocks, rising out of the undulating swell. Behind these, a number of isles become visible, intersected by myriads of bays and inlets. Extensive forests of figs, magnolias, and sassafrasses, interspersed with lime and birch, sweet gum and persimmon, cover the farthest islands; — in many places the trees extend to the sandy shore. The outmost rocks and skerries have but a scanty covering of grass, and many are entirely white with guano and are tinted with faint rosy hues by the first rays of the rising sun. Slowly and leisurely the swelling tides break against the rocky coast. Their metallic coloured surface reflects the glory of the sky, and the varied tints of the tawny rocks, the glaucous tufts of lime-grass, and the dark woods, stand out against the liquid mirror.



Fig. 43. Left femur (f) and tibia (tt) of Pheasant (F) and Loon (L) so as to show the origin of the muscular bundles of the m. gastrocnemius externus and internus on the patella (pa) and the insertion of the tendon on the neck of the tarsometatarsus (tm).

But up there on the skerries, all is astir. Between grass and tussocks, smooth-worn paths lead down to the water. A long, tapering beak appears among the tufts. A supple, snake-like neck follows, and a large torpedo-like body, pushing slowly on, down the path. On every side, above and around in all directions, there is a sliding and scrambling of large, heavy bodies — the yellowish-white bellies glitter in the sun, and their flanks are lengthwise striped with shades of brown. On the back the stripes seem broader and of a bluish-black colour. The head, too, is covered with stripes, but these are connected with small cross-bands, thus producing a series of light strings of pearls across the temples and the neck.

With a little splash the birds slide into the water; — rocking on the swells, flock after flock moves through the straits and channels between the skerries out upon the open sea. The wingless bodies float rather deep in the water; some of them only display a narrow streak of their backs, and on the slim, erect neck, the elongate head turns quickly, first one way, then another. From time to time the whole body submerges, slowly rising to the surface again. One of the birds opens its beak a little, displaying a long row of small, pointed teeth, and utters a strange cry, a deep *huoohuuh*, to which the others respond, repeating and re-echoing it among the skerries.

Suddenly a shoal of argent-tinted fish jump out of the water in the distance, and disappears again. At a given signal, as it were, a number of the birds vanish, as if by magic, without a sound. Only faint ripples on the water denote their whereabouts. Let us follow a couple of them into the deep and see what happens to them there.

Presently the fish are overtaken, and the chase goes on a while beneath the surface. But the fish once more turn up, leaping high into the air. This, however, avails them nothing; they are unable to cope with the speed and agility of the divers. The scaly prey is but small, however, and the appetite of the pursuers voracious; so the birds dive swiftly, their webbed feet working incessantly, in a few seconds they reach the greenish depths.

Here it teems with fish. A large shoal of richly coloured, spotted and striped Pycnodonts are safe. They look like flounders, swimming vertically, and have large mackerel-like tail-fins. To swallow them is next to impossible, and they are full of bones. But behind there is a shoal of turquoise-blue *Sardinoides* with ochrous fins glittering and sparkling; they are medium-sized fish of salmon-like proportions, of which the birds are very fond; and so they rush straight into the midst of the shoal, which hastily disperses.

Both the divers then go deeper and deeper down, swim horizontally for some distance, and rise in front of the shoal. In a flash the toothed beak seizes a fish by the head, . . . a wrench, and the fish is swallowed. The snake-shaped neck darts sideways, and more fishes are caught and quickly despatched. One fish is so large that the two rami of the mandible have to be extended to their utmost limit in order to engulf it. Now they are satiated, their lungs are in need of replenishment, and so they make for the surface.

A large bulk, like some immense leviathan, is swimming about leisurely; it is a great, toothless Ichthyosaur, of which the birds are not afraid in the least, frequently having seen it take toll of the small, repulsive cuttle-fish. Now they sweep so close to its belly that the old fellow gets fairly frightened. With its large vertical tail-fin, it makes an awkward start sideways, — but the divers are already rocking on the waves, inhaling the fresh morning breeze, and they call again, shrilly and loudly, as if mocking at the massive squid-catcher underneath.

The two birds while away some time in the sun; one of them turns on its side in order to rub the feathers with oil. Frequently they dip their pointed beaks in the water, evidently from habit.

All of a sudden they disappear once more in search of prey in the mystic depths. Their torpedo-like form offers but small resistance to the water, and the feathers are pressed tightly to the body, forming an effective water-proof covering by reason of their oily content. With the speed of arrows, the two companions dart through the water, until they reach an elongate, fusiform shape, which apparently can move but awkwardly forward. It is a new-born young one, which the Ichthyosaur left behind when startled by the birds a short time ago.

Both loons immediately attack it, for them a dainty morsel! Its attempts at flight are in vain; it is directly overtaken. Exasperated, it opens the long crocodilian jaws to frighten its antagonists, but these unfold their marvellous grace, strength, and dexterity. They swirl around it, and the unhappy youngster writhes with the agony of its numerous wounds. Now one of the birds has caught hold of the tail-fin and snatches away its uppermost part, while its mate attacks the belly of the little Ichthyosaur, disembowelling it. Both rush upon their luckless victim, so eager to commence their toothsome meal that they contend with each other for their favourite tit-bits.

So engrossed are they in their feast that neither notices the snake-like body, swiftly making its way to the scene of action, propelled by its powerful paddles. Suddenly the mighty jaws, set with strong, dagger-like teeth, opens. They clap on the body of the *Hesperornis*-male; in a flash the slender neck twists round, and the beak picks at the eyes of the reptile, while the triangular webbed feet kick wildly backwards.

But presently the spear-like head sinks limply down, and the water reddens with its blood. With a single snap of his cruel jaws, the Mosasaur engulfs his victim, and the sleek diver glides slowly down the gullet of the reptile.

The other loon has long ago vanished in the distance. Mad with fright, it has rushed away at full speed, seeking shelter in the twilight of the deep. Here a veritable forest of sea-lilies rises from the bottom. On their slender stalks, they wave to and fro in the gentle surge of the depths. The arms, like miniature Ostrich-feathers, are greenish on the outside, and inwardly set with countless purple branches, which, with rhythmical movement, seem to stream down towards the centre of the cup-like body. The frightened *Hesperornis* plunges straight into this fairy wood. Blindly she strikes against

the feathery arms of the lilies in her path, leaving in her wake a trail of dismembered limbs. Others, close by, fold their delicate arms over their cup, making the splendid feather-crown resemble the bud of a water-lily. It looks as if a magic wand had touched the lilies and transformed them completely.

Only the torn and dismembered greenish stalks mark the way taken by the diver. — She is so deep in the enchanted wood that the Mosasaur has long ago lost sight of her, but now the danger is past, exhaustion begins to play its part, and she is at the point of suffocation. She must reach the surface at all costs, and, letting herself go, she rises like a bubble from the depths.

With what joy does the bird once more gain the surface! she opens her throat to the full and takes deep and long breaths. — Refreshed she swims rapidly towards the skerries in the distance. Presently a party of companions are seen approaching. She raises herself upright in the water, trims her feathers carefully, and calls with a loud note. The others answer her call, and proud, like a full-rigged ship, one of them steers in her direction. She turns and flees; he follows, and the pursuit continues, now on the surface, now down in the deep. At last she stops, and the male emerges in front of her. He shakes himself and raises his whole body in the air, — she follows suit. The performance resembles some weird dance. Standing erect on the water, calling and shouting in competition, they keep billing and rubbing each other's neck; the air reverberates with their love-song.

Another male, ever jealous of a rival, rushes towards them and makes a vicious onset on the first. A furious struggle ensues. The two birds move so quickly that it is impossible to tell one from the other. At intervals a long neck is seen curving upward like a snake; now they move across the surface amid a cloud of spray, and now they dive beneath the swell. They have disappeared, but soon emerge far away; one of them screams out loudly, but is again dragged down by his rival. The remaining birds float idly on the roller, impartially watching the fierce struggle, which at last results in the retreat of the challenger, bleeding and bedraggled.

Meanwhile the sun has risen high in the sky, and its warm beams invite rest after the morning exertions. The birds retire to their islets to dose in the sunlight. The long row of necks, rising above the waves, leisurely wending their way thither, is indeed a strange and imposing spectacle.

As easy as it was in the early morning to glide down from the rocks, so troublesome is it to regain them. The birds swim rapidly through the surf and mount the stony beach with a leap, but it is fraught with great difficulties to proceed any farther. They struggle along, amongst the boulders, moving on their bellies like seals. The grace and agility displayed by the birds while in water has now forsaken them. At last each and every one of them has found its place, and a scrupulous inspection of the feathers begins. Some of them stand for a moment on their feet and shake themselves energetically; others lie comfortably stretched out on their sides, trimming the dense plumage of the belly.

Suddenly a large shadow moves across the birds, and a whirr of wings is

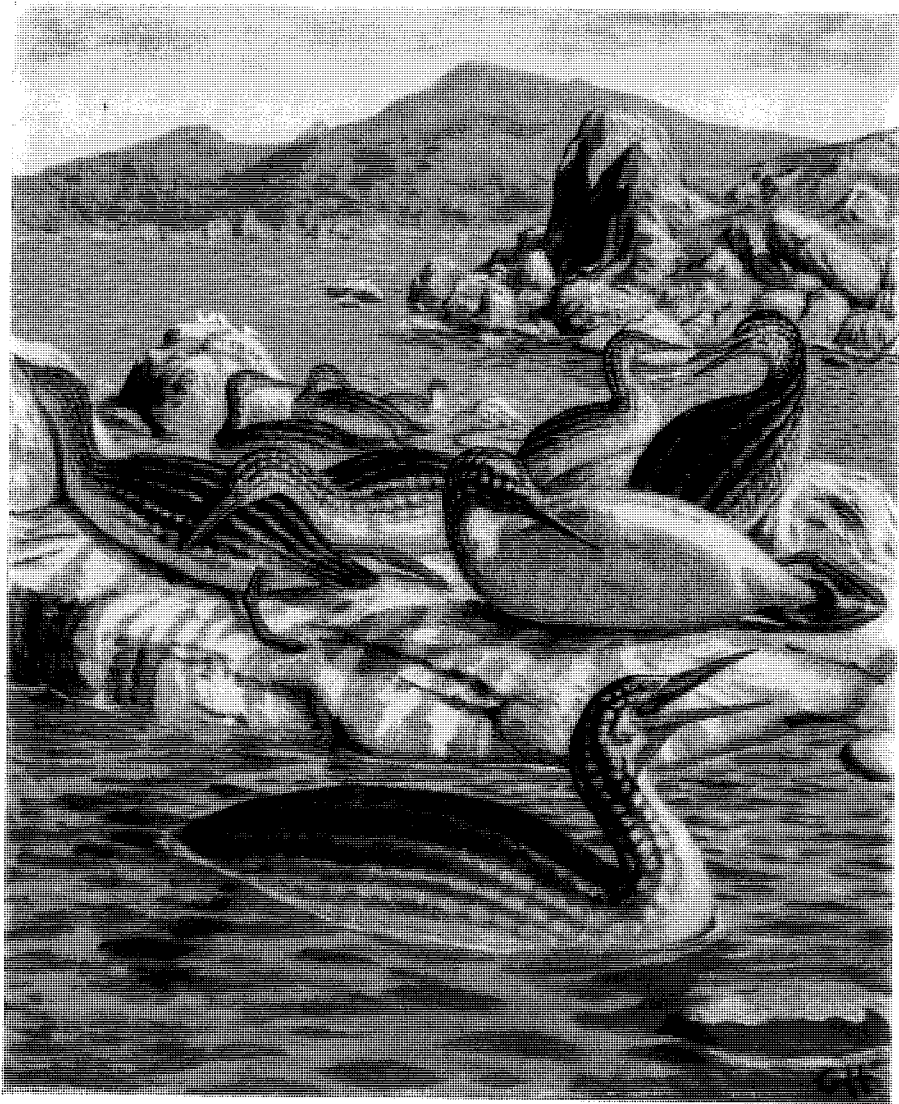


Fig. 44 Restoration of *Hesperornis regalis* on skerries in the Cretaceous sea, painting by the author.

heard in the air. Those lying close upon the water's edge, dive hurriedly in; but the rest raise their heads and cry out. Yet it is a rather commonplace and harmless sight. *Pteranodon*, the gigantic dragon of the air, sweeps low above the birds in a masterful flight. Stupidly they stare after it, little thinking that once their ancestors, too, were capable of moving in the airy breezes. Mocking the birds, the flying dragon returns, and once more its mighty wings whirr above the clamorous loons. The long, tapering beak cuts the air like a spear, and from the crown of the head projects a beak-like crest, some kind of steering device. The body is but small, compared to the marvellous expanse of wings, supporting the *Pteranodon* as easily as if this majestic gliding through the air were mere play.

A swarm of white birds with bluish-grey heads have now descried the soaring dragon and, amidst angry cries, starts in pursuit, at the same time displaying rows of glittering, pointed teeth. It is a flock of *Ichthyornes*, ever jealous of this intruder on their fishing-grounds. On their long, tapering wings, they swirl around it, like swallows round a sea-eagle. Paying no heed to them, however, it pursues its flight higher and higher into the azure sky, until the birds fall off.

With the faint breeze, ever varying in the noon-day heat, the flying fish appear. Shoal after shoal rises above the surface; it is the ruby *Chirothrix*, which in low, long curves glide away, supported by their broad fan-shaped fins, their scaly bodies gleaming in the sunlight. This spectacle catches the eye of the soaring dragon. Suddenly, folding its wings, it descends like an arrow to the sea-level. In a second it is among the flying fish and secures its prey before they again disappear below the surface. Farther away it pursues another shoal; its dimensions grow smaller and smaller, until at last it is lost to sight in the midday haze.

The large crowd of divers has by now quieted down after the disturbance. The cries have ceased, and all the birds are idly dozing in the heat. —

Such life was lived millions of years ago with almost the same fears and the same pleasures as are found to-day.

SUMMARY

The rest of the fossil birds are of no importance to our investigations.

In summing up the resemblances between the fossil birds examined, and the reptiles, we arrive at the following facts:

In the skull there was nothing which could not be matched among reptiles. The sclerotic circle existed in a great number of reptiles; the teeth, found in the upper and lower jaws as well as in the premaxillary, were essentially reptilian; so also the most bird-like features, the large orbit and the large preorbital fenestra. Even the quadrato-jugal bar did not resemble that in birds, but was very much like that of a reptile. The individual bones of the skull had exactly the same position as in reptiles; a quadrate in both connects the skull with the mandible; neither quadrate nor quadratojugal are to be found in

mammals, the mandible of which is chiefly composed of the dentary, while in birds and reptiles the mandibles were quite identical, the two rami of the mandible being separate in both.

From this it is evident that the skull of *Archaeornis* might very well belong to a reptile, but never to a recent bird.

The vertebræ were practically identical, and both had free cervical ribs. There was no difference in the thoracic, nor in the ventral ribs, this last an especially reptilian feature. The tail in no way resembled that of a modern bird, but was long and slender as in reptiles.

The resemblances in the shoulder-girdle were also striking. The pelvis was very small and its individual bones very reptile-like; the sacrum was composed of fewer vertebræ than in many reptiles. The hind-limb also presented remarkable resemblances to that of the reptile, especially in the tarsus and metatarsus, contrary to what has hitherto been stated.

Though the fore-limb supported a wing, the carpus was very different from that of a recent bird, and in reality very similar to that of the reptiles; in the hand the whole reptilian basis was still persisting. The digits were the same, and each one of them had the same number of phalanges as those of a reptile; the digits all bore claws.

From its remains, *Archaeornis* may be characterized as a reptile in the disguise of a bird.

This is what the skeletons of fossil birds tell us. But the skeleton is only the inner framework of the animal; so we must examine the softer parts, too, and mark the stages of development of the whole animal, before it is possible for us to reach a final conclusion. In Part II, therefore, we are going to compare the embryonic stages of bird and reptile; in Part III, some anatomical and biological features of both classes; and finally, in Part IV, we shall make an attempt to find the ancestor of birds and its relations.

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- (4*) As Petronievics has the priority in describing the pubic bones of *Archaeopteryx* it is of course decisive when he calls the hole in the proximal part of the pubis proper: *foramen obturatorium* (4, Tafel I). But in this way some uncertainty in the nomenclature has arisen because the fenestra between the ischium and the pubis in mammals is also named *foramen obturatorium* and some authors have called the same fenestra, when occurring in certain birds and reptiles, *foramen obturatorium*. Wiedersheim (5) calls the hole in the pubis proper of existing reptiles: *foramen obturatum* and the fenestra between the ischium and the pubis *foramen pubo-ischadicum*. The same fenestra in mammals he calls: *foramen obturatum*.
- (5) WIEDERSHEIM, R., Vergleichende Anatomie der Wirbeltiere, Siebente Auflage, Jena 1909, illustrates on p. 152 the skull of a duck seen in profile, in dorsal, and ventral view. Here the hindmost part of the nasal (which in my fig. 3, 3 is lettered N) is called frontal; the frontal is then called parietal and the parietal supraoccipital. A young student of anatomy gets by this a rather wrong impression of the bird's skull, and this illustration being reprinted in seven issues of the book, he must perforce suppose this interpretation of the bones to be the right one. This has also Dr. M. Hilzheimer evidently believed, for in his "Handbuch der Biologie der Wirbeltiere, Stuttgart 1913" he has on p. 384 reproduced the skull from Wiedersheim and with the same errors.
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- (19) PETRONIEVICS, B., Ueber die Berliner Archaeornis, Genf 1925. Not till my Part I was in print did I learn of this new paper by Petronievics. The results of his renewed examination of the fossil are as follows: Of the skull he gives no restoration, nor does he mention the detail of the important left side of same. His sketch of the right side of the skull, I am unable to understand, and it seems to me to bear only a slight resemblance to the original. According to the preparation of the cervical vertebræ by Prof. Tornier, he states that these are biconcave. He thinks it possible to distinguish 12 pair of ventral ribs. The number of caudal vertebræ in *Archaeornis* is 20, while *Archaeopteryx* has 21.

The coracoid he believes to be that of a typical carinate bird, while he names that of *Archaeopteryx* a typical ratite coracoid. The clavicles of *Archaeornis* do not seem to have coalesced into a furcula. What Dames thought to be the transverse section of the sternum, Petronievics regards as the longitudinal section of a part of the right half of the sternum. He has drawn a restoration of this very small sternum, it forms an inverted broad isosceles triangle; its position, according to his view, was in front of the ventral ribs and it articulated only with two thoracic ribs.

He has found but three carpals, a distal one, a radiale, and an ulnare. The presence of a pubic symphysis, he considers out of the question in *Archaeornis*, and further that the distal end of the pubis is very different from that of *Archaeopteryx*. What I have named x in my fig. 9, III, Petronievics regards as the well preserved proximal end of the pubis. Like myself, he has found a distinct fibulare. He has also been able to make out a tibiale and a distinct intermedium, in *Archaeopteryx* ascending the anterior face of the distal end of the tibia. The distal tarsals are wanting, and Petronievics thinks that they have separately coalesced with the proximal ends of the three metatarsals, just as I thought was the case (p. 24), and, like myself, he considers the metatarsals wholly separate.

PART II

EMBRYONIC STAGES OF REPTILES AND BIRDS

THE GERM CELLS

THE period of an animal's development, from the earliest discernible germ (primordium) until a certain degree of maturity, is called the embryonic stage. The embryo has spent this period, either within an egg-shell, or within the body of its mother. The history of this stage is called Ontogeny.

All animals are composed of cells, forming a colony and varying in form and substance. Some of the cells are different from the others in being able to escape from the colony and start the development of a new colony, or new multicellular individuals. These cells are called germ-cells, and they are specialized for the performance of their respective functions as sperm-cell (spermatozoön) and egg-cell (ovum).

The mobile sperm-cell is active and impregnating, while the egg-cell is passive and receptive. The sperm-cell generally consists of three distinct sections: head, neck, and tail, the last being capable of vibratile motion, by means of which the sperm-cell is rather rapidly propelled through the juice. How the sperm-cell of the different classes of animals looks, is shown in fig. 45. W. Waldeyer (1) says about those of the birds: "Two forms of sperm-cells may be distinguished; one of these is typical of most species of birds, and is akin to those of the reptiles, the other one, peculiar to Perching Birds (*Passeres*), may approximately be ranged with those of Amphibians, Sharks, and Rays".

When looking at fig. 45, we are at once struck with the fact that the sperm-cells of the mammals differ considerably from those of the other classes of animals, while those of the various species of mammals themselves are almost homologous. In this respect, man is a genuine mammal (fig. 45, 36); his sperm-cell is here shown from two sides; the head is flat and oval, somewhat pear-shaped in side view. Those of other mammals are very similar: the sperm-head is broad and compressed, thus differing widely from that of the birds. In these, on the other hand, the resemblance to that of the reptiles is very considerable. In both of these classes, the sperm-head is a rather elongate small cylinder, in front usually tapering like a needle. Ballowitz (2) has examined these sperm-cells very closely and, referring to the reptiles, says about the inner structure of the sperm-head, as follows: "It seems to me that we here find a structure similar to that of many birds, e. g. *Vanellus*, *Cuculus*, etc." The cross-streaked central part of the sperm-neck of Snakes (*Ophidia*), is due to spiral formations enclosing the axial filament, and it is surrounded by a protoplasmic sheath. This structure very much resembles that of the sperm-neck in the Pigeon (2). As a matter of fact, the resemblance between the sperm-cell of the Common Viper, and that of the Pigeon, is also very striking

(fig. 45, 12 and 22), especially when the difference in the appearance of the two animals is taken into account. The spiral film, enclosing the axial filament, is very easily broken, and possibly that is the reason why it is so little conspicuous in the sperm-cells of several birds. The apparent difference that

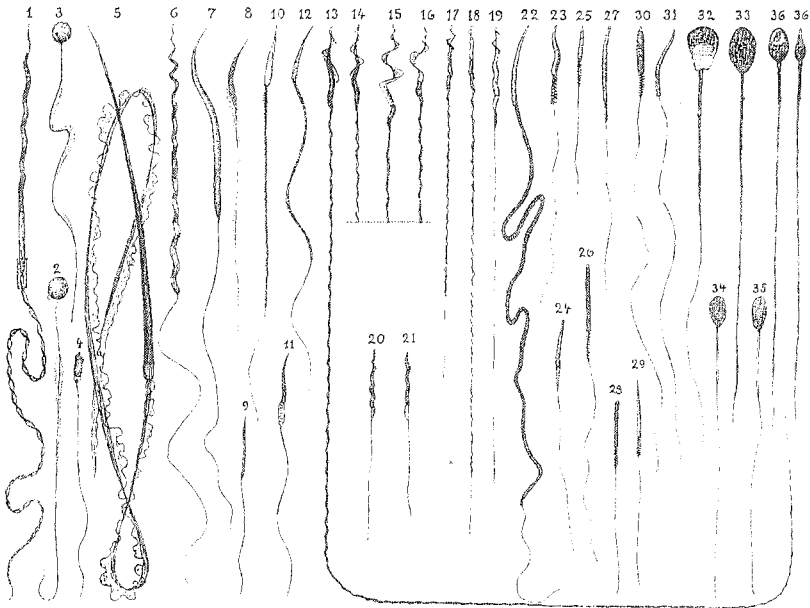
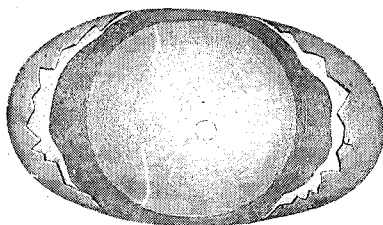


Fig. 45. Spermatozoöns of different vertebrates; fishes (1—4), amphibians (5—7), reptiles (8—12), birds (13—21), and mammals (32—36). 1 Ray, 2 Perch, 3 Pike, 4 Sturgeon, 5 Three-toed Salamander, 6 Toad-Frog, 7 Tree-Frog, 8 Lizard, 9 Slow-Worm, 10 Common Snake, 11 Land-Tortoise, 12 Common Viper, 13 Chaffinch, 14 Greenfinch, 15 Flycatcher, 16 Redstart, 17 Tree Warbler, 18 Martin, 19 Golden Oriole, 20 Red-backed Shrike, 21 Rook, 22 Pigeon, 23 Nightjar, 24 Spotted Wood-pecker, 25 Cuckoo, 26 Black-headed Gull, 27 Black Kite, 28 Lapwing, 29 Sheldrake, 30 Common Turkey, 31 Common Fowl, 32 Guineapig, 33 Bull, 34 Dog, 35 Cat, 36 Man, flat side and profile. Tails of 14, 15, and 16 docked; 13 in full length, its nat. size is 0.235 mm. 2, 3, and 36 after G. Retzius, 5 after Mc. Gregor, 7 after La Valette St. George, 8 after Leydig, 32 after Meves, the rest after Ballowitz.

strikes us in the sperm-cells of the Perching Birds, is evidently nothing but a further development of what is found already in the other species of birds. The head is of the same primary form in both cases, but in the former species it is either enclosed in a very thin spiral film, or the head itself has the form of a corkscrew. This transformation will prove to turn out very differently; in the case of the Rook, for instance, it is but very little conspicuous. The axial filament of the tail, as also the spiral film enclosing same, is found in proportion to be exceedingly long in some species, and from this very peculiarity we are able to judge of the cause to which it is due. To such a screw or corkscrew, only one manner of locomotion is possible, i. e. the rotatory one. Several investigators, especially Ballowitz (2), have also been able to prove such a rotation in sperm-cells of birds. It is the axial filament of the

Fig. 46. Egg of Alligator, from above. The opened shell with broken borders is seen and within these the white shell cuticle. In the middle the yolk-sphere and nearly in the centre of this, the little whitish germinal disc. The darker part surrounding the yolk is the white; after Clarke, $\frac{2}{3}$ nat. size.



tail that produces the motion, the many fibres of which it consists contracting, thus making it vibrate like a fiddle-string. By the form of the head, this vibratory power is transposed into a rotatory and progressive motion. Not only in the case of Perching Birds, has Ballowitz observed this screwing motion, but also in sperm-cells of the Common Fowl, the Sheldrake, and the Lapwing. This also holds good of the reptiles, while the very form of the sperm-head of mammals makes such a locomotion impossible. We shall understand this better when taking into account that the copulation of mammals differs considerably from that of birds and reptiles. As far as the two latter classes are concerned, the sperm-cells have a comparatively much longer distance to travel within the sexual organs of the female before reaching and joining the egg-cell.

The original egg-cell of all animals is alike, and the egg is developed from same in the female sexual gland, the ovary. W. Waldeyer (1) expresses himself to this effect: "The incipient stage of the ovary of birds is exactly like that of reptiles, and the formation of the egg is completed in the same way". In the reptiles, both ovaries are usually in operation, but in birds, generally the left one only. It is, however, not so very rare to find both ovaries developed in various birds of prey.

In the egg-cell of all animals, we find the simple, typical cell-structure; but the egg, when mature, has often assimilated a great quantity of reserve materials, a store of nourishment for the embryo during its development. Hence a very marked difference appears, between birds and reptiles on the one hand, and mammals on the other. The egg is very large, as far as the former classes are concerned, sometimes even enormous (the Ostrich, the Dinornis, the *Aepyornis*), owing to abundant deposits of reserve materials. In the egg

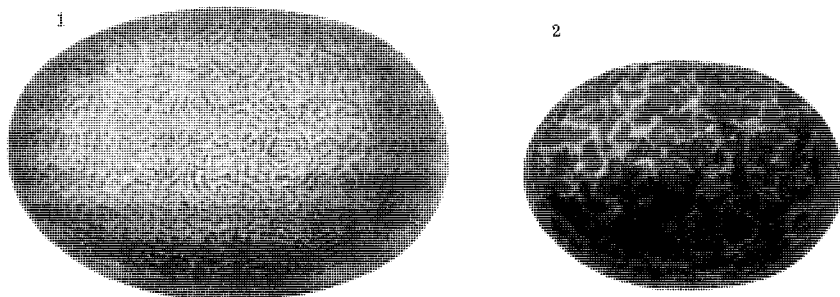


Fig. 47. 1 Egg of Crocodile after Voeltzkow, slightly reduced. 2 Egg of a bird, *Guira guira* (*Crotophaga*) photographed for this work by Dr. R. W. Shufeldt from a specimen in the collection of E. J. Court, Washington, nat. size.

of mammals, on the contrary, the yolk is but small because, during the entire embryonic development, it is joined to its mother and nourished by her.

The reserve materials, deposited in the egg of birds and reptiles, are heavier than the other parts of the cell and, consequently, sink to the bottom of the

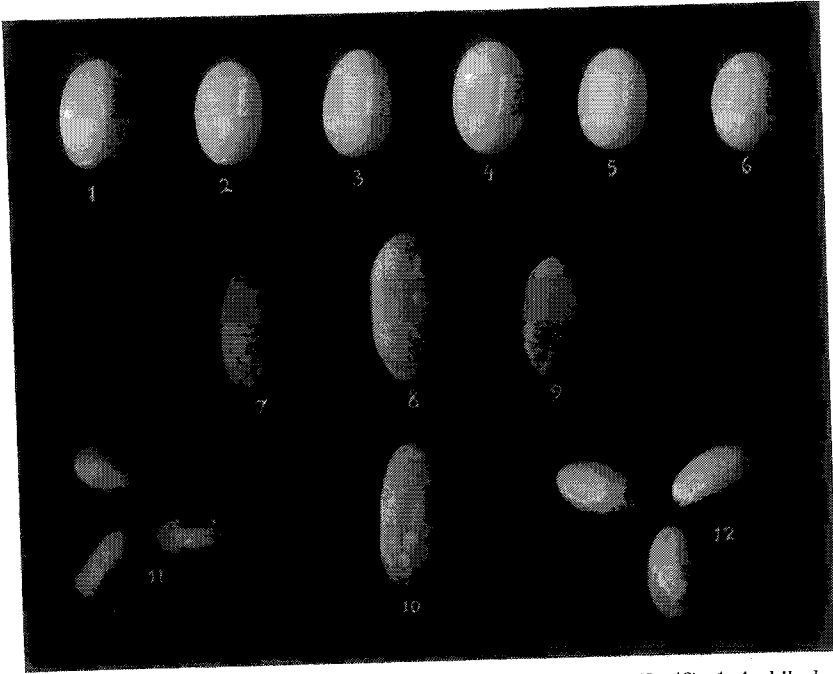


Fig. 48. 1—6 Eggs of Humming-Birds compared with eggs of reptiles (7—12). 1 *Archilochus colubris*, 2 *A. alexandri*, 3 *Calypte costae*, 4 *Selasphorus platycercus*, 5 *S. alleni*, 6 *Stellula calliope*, 7 *Carpophiopus amoenus* (a snake); 8—12 eggs of lizards; 8 *Cnemidophorus sexlineatus*, 9 and 10 *Sceloporus undulatus*, 11 *Liolopisma laterale*, 12 *Anolis carolinensis*; all photographed for this work by Dr. R. W. Shufeldt; the eggs of the Humming-Birds from specimens in the collection of E. J. Court, those of reptiles from the collection of U. S. National Museum; all nat. size.

egg, so that they are kept distinctly apart from the rest, and from the nucleus of the egg-cell, which will always float on top like a drop of oil on water. This part is called the germinal disc, or blastoderm, and it is from this one that the formation of the embryo takes places after the fecundation of the egg. When a Hen's egg, lying on the side, is opened, the blastoderm may be seen, with the naked eye, as a whitish disc on the top of the yolk. That the same holds true of the reptile's egg is shown in fig. 46.

It is the so-called yolk, of which the egg-cell proper consists, which is generated in the ovary. All the other parts of the mature egg, in both classes of animals, are formed in the excretory duct of the sexual gland, the oviduct. In the upper part of same the egg encounters the sperm-cells, and is impregnated by these. In its next phase it is enclosed in layers of albumen, and farther down the oviduct the salts of lime are secreted, which are to enclose the

finished egg as a solid shell. Such a lime-shell we find in the crocodiles, most tortoises, and many snakes. Its chemical ingredients are the same as those in birds; its inner structure, too, resembles that in birds very much, an inner or mammillary layer (Nathusius, 3), and numerous pore canals, being found in both classes. The surface of the shell, however, is generally more rough than that of birds. But within the sub-family of *Crotophaga*, species are found, the egg of which, on the outside, are marbled from thick and rough coverings of lime, similar to the eggs of reptiles (fig. 47). Nor is the typical "ovate" egg, which is the most common bird's egg, found in all cases, and in figs. 47 and 48, examples are given of shapes approximating those of reptiles. Besides the eggs shown in fig. 48, those of the Tuatera (*Sphenodon*) and the Moorish Mud-Tortoise (*Clemmys leprosa*) remind one of the shape of the Humming-bird's egg. This similarity, however, must rather be looked upon as a mere curiosity to which hardly any importance can be attached.

FECUNDATION AND GERM-LAYERS

Owing to copulation, and to the large size of eggs in birds and reptiles, it involves considerable difficulties to study the progress of the very first stages of fecundation in these animals. While thus the Hen's egg most frequently has been used as the object of investigation in showing the subsequent development of the embryo, the maturation and impregnation of the gallinaceous bird's egg is comparatively unknown.

Fortunately, we have the result of an investigation by E. H. Harper (4), acquainting us with the impregnation and fertilization of a Pigeon's egg; according to same, I have drawn four small illustrations in fig. 49. The first one of these is to show how the sperm-head, after having entered the germinal disc, is transformed into a sperm-nucleus. Moreover, the maturation of the egg is shown by two different maturation spindles, and we see the sperm- and egg-nuclei in close contact just before their final unification. The last four little cuts in fig. 49 show similar development of reptiles' eggs: various forms of sperm-head within the egg-cell, two maturation spindles, and sperm- and egg-nuclei in close contact.

The first result of impregnation is that the egg-cell divides into two daughter-cells. These subdivide further: the two become 4, the four 8, the eight 16, etc., so that a large number of cells is rapidly produced. This transformation is called the cleavage of the ovum, and fig. 50 illustrates how this process is carried on in the different vertebrates. As will appear, the principal features are alike in all, and the apparently great differences are due to the larger or smaller quantity of nutritive yolk. A structure obviously very primitive, we find in the *Amphioxus*, the lowest of all "vertebrates" we know of, for it has no vertebræ, but only an internal axial stiffening, called notochord (*corda dorsalis*). In this fish-like creature, cleavage takes place quite regularly throughout the entire bulk of the egg (fig. 50 A). The fact is that there is no yolk to hinder this process, and the result is a ball, in the form of a mulberry, the

cavity of which is filled with liquids. In mammals there is no nutritive yolk either, and the process of cleavage, therefore, exactly corresponds to that of the *Amphioxus*. In the egg of a Frog (B), a distinct difference is traceable between the pole in which the fecundation has taken place (in fig. the upper one), and the other half containing the yolk. Hence, the process of cleavage becomes somewhat heterogeneous. In eggs of fishes with a large yolk-sac, e. g. Sharks and Rays, this heterogeneity is so marked that cleavage commences discoidally, proceeding from the germinal disc, whence it spreads as a thin cellular layer along the surface of the yolk. As birds and reptiles have a very

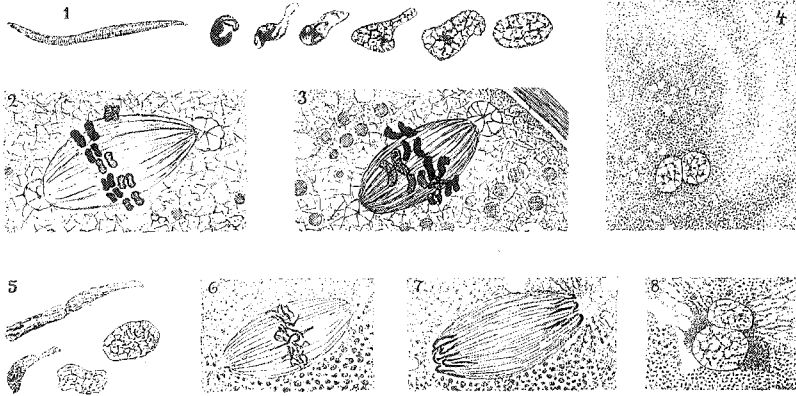


Fig. 49. Details of the impregnation and fertilization of a pigeon's egg; 1 stages in the transformation of sperm heads into sperm nuclei after having entered the germinal disc; 2 and 3 the two first maturation spindles; 4 the sperm nucleus in contact with the egg nucleus; after E. H. Harper. 5 Stages in the transformation of sperm heads within the germinal disc of Common Snake, 6 and 7 two maturation spindles, and 8 sperm and egg nuclei in contact, of Slow-Worm; after A. Oppel.

large nutritive yolk, which does not cleave, the primary stages of cleavage will generally take place on a slightly curved surface, by which the mutual resemblance of cleavage in the two classes becomes very striking (fig. 50 D-H). That cleavage is discoidal, however, does not involve any essential difference from that of the other vertebrates.

Fig. 51 shows sections through the blastoderm during cleavage, in reptiles and birds. The process proves to be alike in both, the cells cleaving not only vertically, but also horizontally, so that the small cells gradually form several layers. Fig. 51 is not intended to give an exact representation of cleavage in all cases, for the clefts vary considerably even in eggs from the same hatch.

What we have so far seen of the development of the embryo, is nothing but the activity resulting in the increase of cells; from the one cell, many are evolved. But from this time on, a very important change takes place, viz. the differentiation among groups of these cells. Larger and smaller sections of cells now become distinguishable from one another; they attain a peculiar form and arrangement, and the first preformation of special organs appears.

The setting in of this stage may best be seen in the egg of the *Amphioxus*, because of its simple and primitive cleavage. A vertical section of same shows

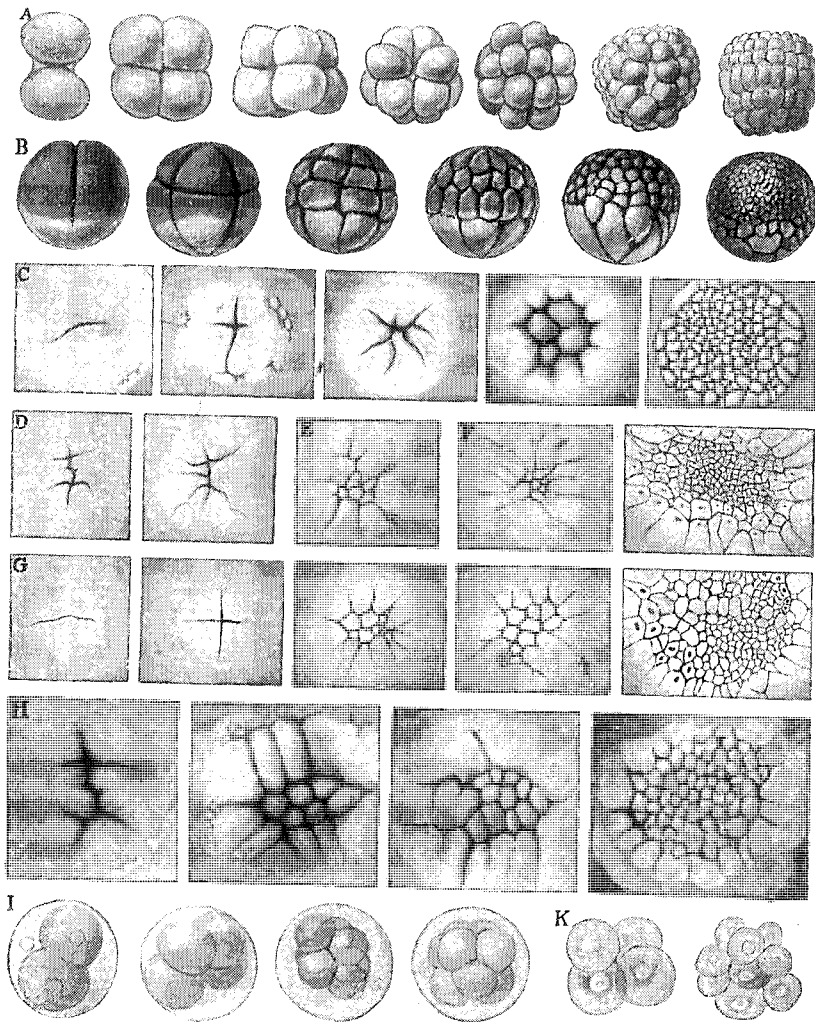


Fig. 50. Stages of cleavage of the ovum in different animals. A *Amphioxus* in different views after Hatschek and Wilson; B Frog, the germinal disc (blastoderm) is in the upper pole, after Morgan; C Electric Ray after Rückert; D Lizard after Kupffer; E Tortoise after Clark. F Slow-Worm after Oppel; G Hen after Kölliker; H Pigeon after M. Blount; I Sheep after Assheton; K Bat after Duval. A, B, I and K show the whole ovum, C—H only a part of the blastoderm, seen from above.

a ball filled with liquids, the walls of which consist of a single layer of cells; this ball is called blastula. Just as we can make a depression in a soft rubber ball, a part of the surface cells of the blastula begins to inflect towards the centre, and gradually it takes the shape of a bowl with double walls, the gastrula (fig. 52, 6). The two walls are called germ-layers, and we distinguish between the outer layer, the ectoderm, and the inner layer, the entoderm, both of which are of immense importance for the subsequent formation of organs. The opening of this gastrula is called primitive mouth

or blastopore, and the inner cavity primitive intestine or archenteron.

A mere glance will suffice to show that the formation of the gastrula in eggs containing a large nutritive yolk, cannot exactly correspond to that of the *Amphioxus*.

We have seen that the result of cleavage in reptiles and birds is the formation of the blastoderm, a flat expansion of cells on the top of the yolk.

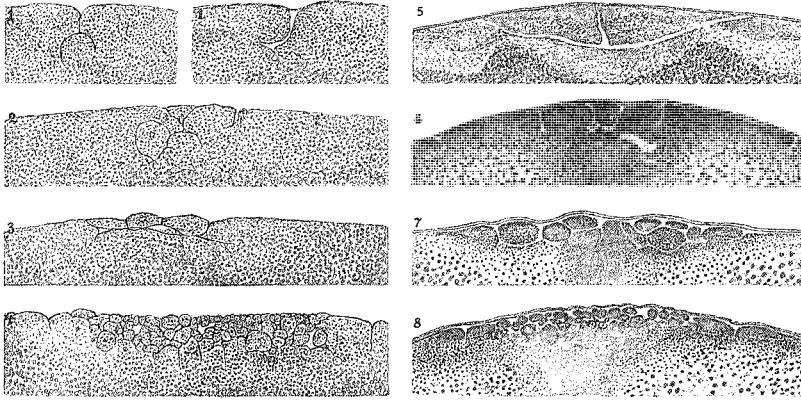
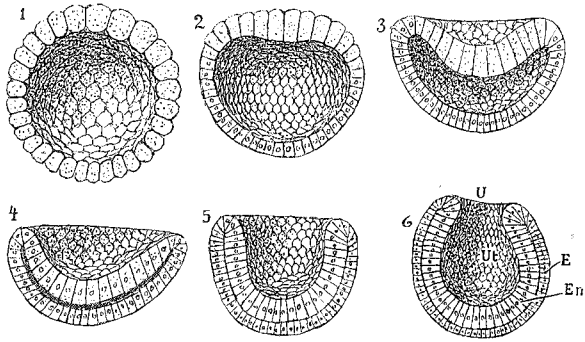


Fig. 51. Transverse section of the blastoderm during the primary cleavage in reptile and bird. 1—4 Lizard after Sarasin; 5 Hen after Oellacher; 6—8 Pigeon after M. Blount.

In the Pigeon's egg, this process will now be as follows: The cells of the blastoderm posterior to the centre, will spread out so as to form a single layer, while the anterior portion is many cells thick. The thinning process will result in the formation of a cavity below the blastoderm, corresponding to the one shown in fig. 52. The cells of the posterior margin of the blastoderm will now remove from the yolk, and this margin turn inward and extend anteriorly towards the centre of the blastoderm, so as to form an inner layer of cells bounding the cavity and becoming the primary entoderm. The space between the margin and the yolk is the primitive mouth, and the new cavity the primitive intestine (fig. 53). At the margin of the primitive mouth the ectoderm and the entoderm join, as shown in fig. 52. The primitive mouth in the Pigeon's egg closes just before the egg is laid.

The three other illustrations in fig. 53 will show transitional stages between the gastrula in *Amphioxus*, and the changes of the gastrula, we see in the bird. In the Salamander, the yolk is not so large that it causes any essential changes in the formation of the germ-layers. But in the Worm-like Amphibian, the development of whose egg in many ways is similar to that of the reptiles, having likewise a very large nutritive yolk, cleavage is discoidal, and the formation of the entoderm, therefore, closely resembles that of reptiles and birds. Fig. 53, 2 shows the incipient formation of the entoderm (En). In the Lizard, we can also see the opening between the ectoderm and the entoderm, as also the transition between these at the closed primitive mouth.

Fig. 52. 1—6 The development of the egg of *Amphioxus*; the egg is cut through. In 3 the forming of the gastrula has commenced; E ectoderm, En entoderm, U primitive mouth, Ut primitive intestine; after Hatschek.

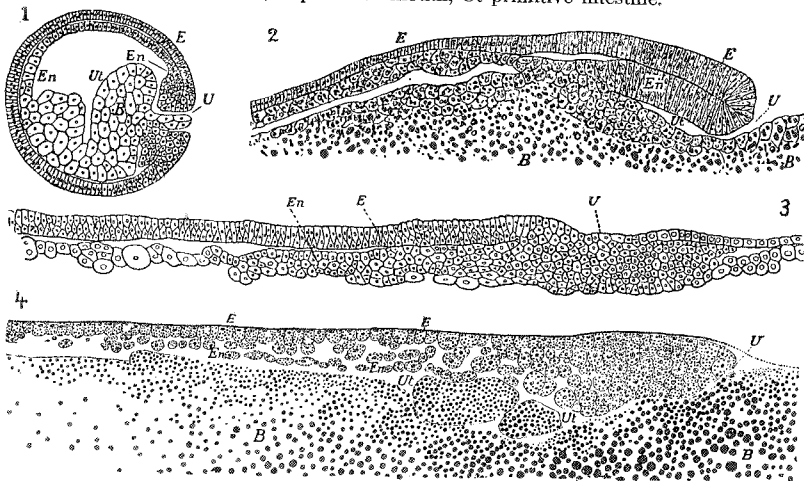


During the first hours' incubation of the bird's egg, there is a thickening of the cell-layers of the ectoderm about the centre of the germinal disc. The back part of this thickening, as seen from above, has the appearance of a slightly opaque band, which increases rapidly in the posterior direction, and is called the primitive streak (fig. 54, D and H).

The process of development in reptiles is exactly like that of the birds. It is also in the central part of the germinal disc, in the ectoderm, that a thickening sets in, from the hindmost part of which a small process may be seen, called the primitive streak (fig. 54 L). It has not the same form as that of the bird's egg, but is usually shorter and broader; as a whole, the outer appearance of the primitive streak varies considerably in the different species of both birds and reptiles. But in its component parts and general bearings, the primitive streak in reptiles is exactly homologous to that of birds and mammals (O. Hertwig, 5).

The primitive streak in birds, then, is a thickening of the ectoderm, and

Fig. 53. Longitudinal section of egg and germinal disc of two amphibians, a reptile and a bird to show the gastrula-stage in these. 1 Salamander; the whole egg, after O. Hertwig, 2 Worm-like Amphibian (*Hypogeophis*) after Brauer, 3 Lizard; the primitive mouth closed, after Weldon, 4 Pigeon; only the hindmost part of the germinal disc shown, after Patterson. B yolk, E ectoderm, En entoderm, U primitive mouth, Ut primitive intestine.



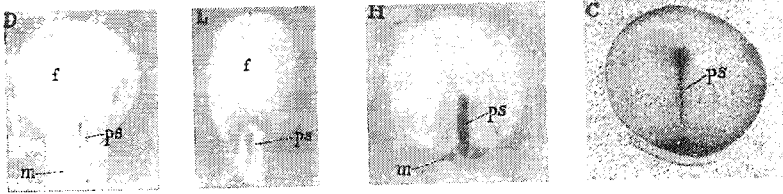


Fig. 54. Midmost part of the germinal disc in eggs of D Albatross (*Diomedea*) after Schauinsland, L Lizard after Will, H Sooty Tern (*Haliplana*) after Schauinsland, C Dog after Bonnet; f thickening of ectoderm, m outgrowth of mesoderm, ps primitive streak. D and L show the first appearance of the primitive streak.

by emigration of cells from same, a new germ-layer originates, the mesoderm (fig. 55 M). At the hindmost end of the primitive streak, the mesoderm broadens out considerably (fig. 54 D, m), and same will often appear as a sickle-shaped end of the primitive streak (fig. 54 H, m).

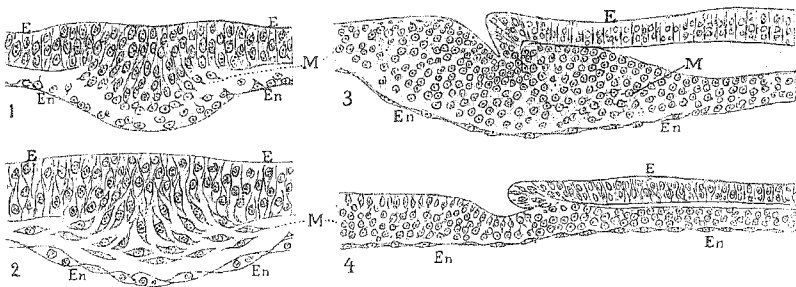
"In reptiles, too, the mesoderm owes its origin to the primitive streak, which also here is developed from the ectoderm. This is particularly traceable in the Chameleon (fig. 55). In the Tuatera (*Sphenodon*), the Lizards (*Lacerta*), and the Turtles (*Chelonia*) exactly similar conditions prevail" (Schauinsland, 6).

The homologue of the origin and arrangement of the mesoderm, in both reptiles and birds, is strikingly illustrated in fig. 55, showing transverse and longitudinal sections of a piece of the primitive streak in both classes. The differences are no greater than those of the different species of birds themselves. The transverse sections show the cells emigrating from the ectoderm (E), and how these form the beginning of the mesoderm (M). The latter is entirely separate from the entoderm (En).

As the primitive streak gradually lengthens, a projection appears in the very foremost parts, the head-process (fig. 56 Ht), and round this one as a centre the embryo develops (fig. 56 FA). As the embryo grows in length, the primitive streak diminishes, until finally, when the tail-fold is formed, it disappears altogether.

From the three germ-layers the following organs originate: From the ectoderm originates the outer skin with its multifarious formations, e. g. hair, nails,

Fig. 55. 1 and 2 transverse sections of the primitive streak of 1 Chameleon, 2 Sparrow; 3 and 4 longitudinal sections of a part of the primitive streak of 3 Tuatera (*Sphenodon*), 4 Sparrow, all after Schauinsland; E ectoderm, En entoderm, M mesoderm.



scales, horn, and feathers; moreover, sebaceous, sudoriferous, and lacteal glands; finally, the central and peripheral nerve system and the most important parts of the sense organs, the optical cells, the auditory and olfactory cells, the lens of the eye.

The entoderm constitutes the point of departure for the intestinal canal, including the cavity of the mouth and the teeth, the tongue and the salivary glands, the gullet, the stomach, the large and small intestines with their characteristic suspensory ligaments, various glands attached to same, the liver and the pancreatic glands, the thyroid gland, the lungs. From this germ-layer also the notochord (*chorda dorsalis*) originates.

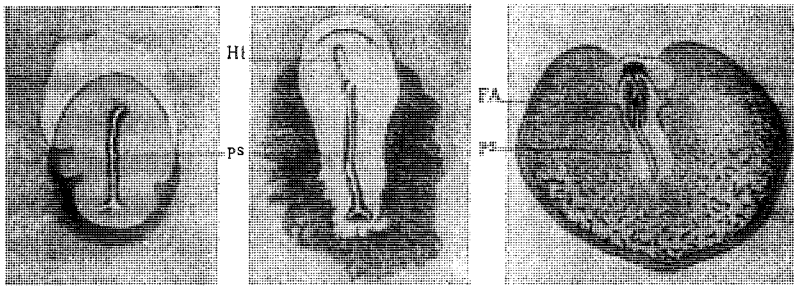


Fig. 56. Three stages of the germinal disc in the egg of a Hen. The first shows the primitive streak (ps) in the thickening of the ectoderm, in the second the head-process (Ht) has appeared, and in the third the preformation of the embryo (FA) has commenced to develop round this; after Lillie. All viewed as transparent objects.

From the mesoderm are evolved most of the muscles, the urinal and sexual organs, and the mucous membranes, which cover the cavities of the body. Finally originates, generally a little later than the other germ-layers, the so-called mesenchyme, which is composed of emigrated cells, and from this originates fibrous tissue, cartilage, bones, ligaments, sinews, blood and lymph vessels, the spleen, medullary substance, besides a great part of the muscles.

In course of time the germ-layers grow round and enclose the nutritive yolk of the embryo, and the resulting formation is called the yolk-sac.

About the blood-vessels of the yolk-sac, Schauinsland (6) remarks that, even though they are not so well known in reptiles as in birds, we may definitely maintain that the correspondencies between these two are striking. Moreover, he thinks that the existing differences, not merely between these two classes, but also between the individual orders of same, are insignificant.

The further development of the embryo is shown in figs. 57 and 58. In order to include as many animals as possible, only the primitive streak and preformation of the embryo with their immediate surroundings are illustrated. The horizontal columns show the same stage of development in the different animals, so far as it is possible to do this, for the different stages are reached earlier in some, later in others. The vertical columns illustrate the progressive development, i. e. the exterior transformations of the embryo as shown by

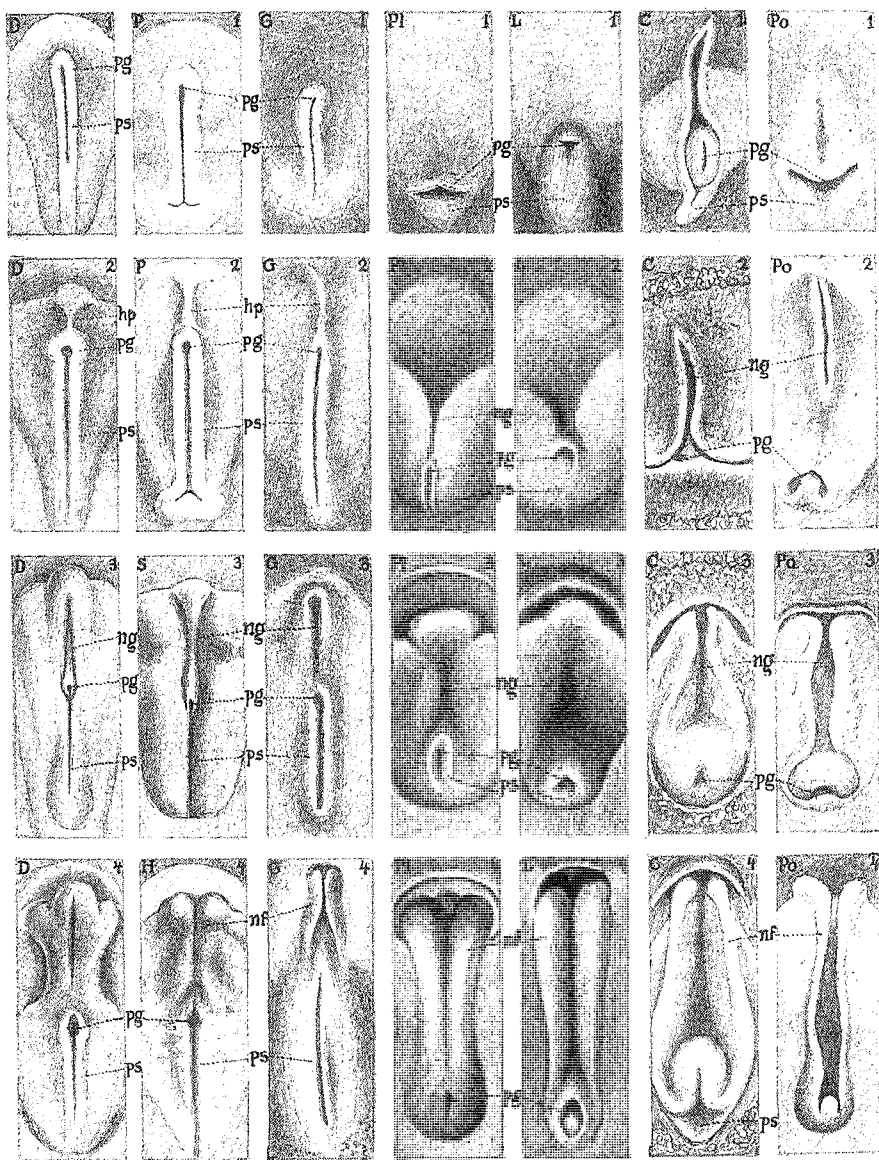
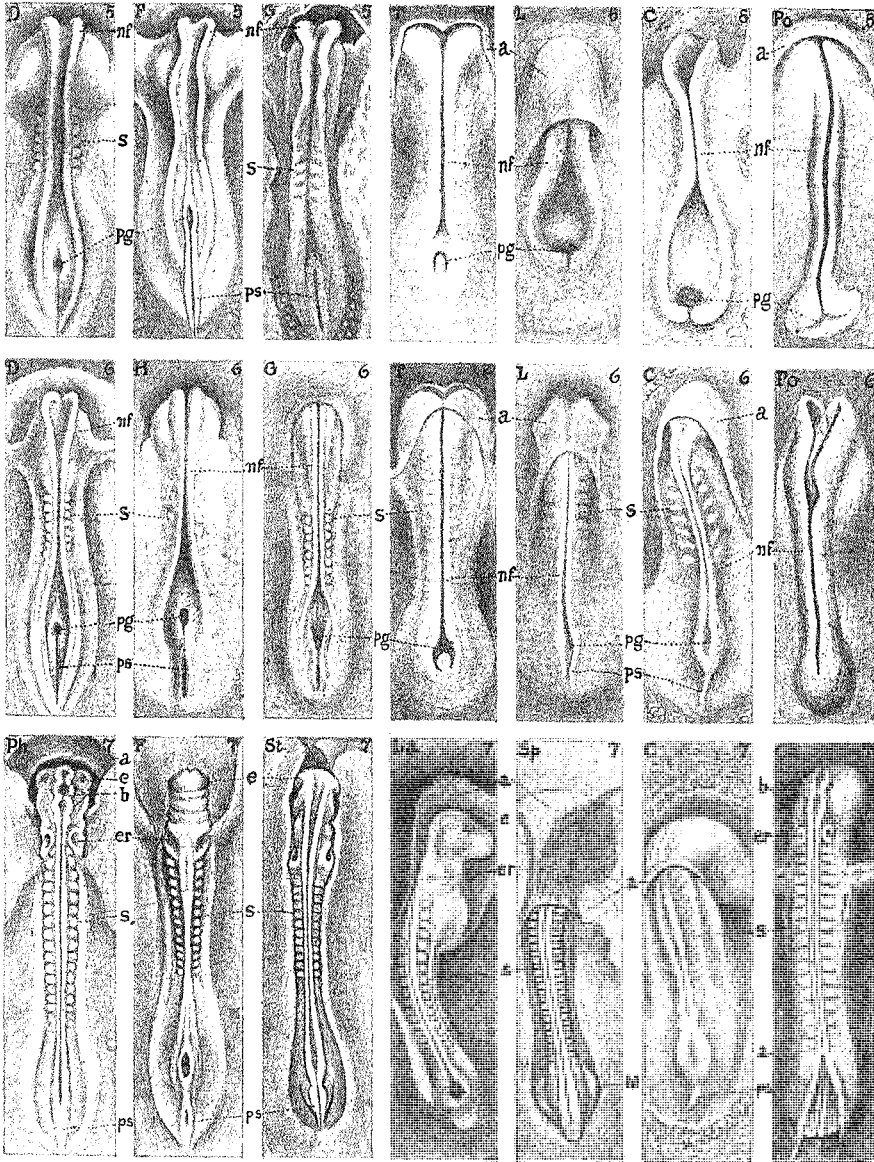


Fig. 57 and 58. Embryos of birds and reptiles in early stages. Only the primitive streak and the preformation of the embryo are represented. The horizontal series show the same stage of development, the vertical the progressive evolution (1—7). The three left columns are birds, viz: D Albatross (*Diomedea*), F Frigate-bird (*Fregatus*), G Hen (*Gallus*), H Sooty Tern (*Haliplana*), P Sparrow (*Passer*) Ph Tropic-bird (*Phaëthon*), S Gannet (*Sula*), St Starling (*Sturnus*); G after Hertwig and Keibel, the others after Schauinsland. — The four right rows are reptiles, viz: C Crocodile, Ch Turtle (*Chelonia*), L and La Lizards, Pl Gecko (*Platydictylus*), Po Arru Tortoise (*Podocnemis*), Sp Tuatera (*Sphenodon*), T Soft Tortoise (*Trionyx*); C and Po after Voeltzkow, Ch and T after



Mitsukuri, L and Pl after Will, La after Peter, Sp after Schauinsland; — a amnion (a membrane investing the embryo), b preformation of brain, e eye, er ear, hl hind-limb, hp head-process, nf neural fold, ng neural groove, pg primitive groove, ps primitive streak, s somites. In Sp 7 the amnion is cut away from the lower half of the embryo, in Ch 7 it covers nearly the whole embryo with the exception of a small triangle below and in La 7 it is cut open so that the embryo is detached. All the illustrations are by reflected light in dorsal view, the upper part of the embryo in La 7 is turned so that the head is seen in profile. C 7 shows the commencing cervical flexure seen in fig. 60.

reflected light. Viewed as transparent objects, which is very common in microscopes, the illustrations will be entirely different (compare fig. 56 with fig. 57 G, 1 and 2; see also fig. 64 G and Ac).

It strikes us at once that the exterior of the primitive streak does not seem to show any similarity at all between the two classes. The differences also between the various reptiles seem to be considerable; the birds appear to be more homogeneous, but the correspondence cannot, in their cases, be considered perfect either. However, if by the aid of the lettering we compare the corresponding parts and look at the progressive development, we shall find that, in reality, this difference is but an outer one; — the same foldings occur, and these bring about the same results, so that the embryos of Nos. 6 and 7 are almost homomorphous.

The first horizontal column (fig. 57, 1) shows the primitive streak (ps), through the central line of which, in the case of birds, there is a groove, the primitive groove (pg). It is bounded by the primitive folds and terminates in front, in the primitive pit. To which part the primitive groove corresponds in reptiles, may be found by examining the micro-sections, the entire germinal disc, as mentioned before, consisting of the ectoderm, the entoderm, and the mesoderm, in both classes of animals. In the case of reptiles, this primitive groove will most frequently appear as a transverse cleft (Pl 1 and Po 1, pg); the primitive streak itself is broader and usually of a less distinct form. In more progressive stages, however, this primitive streak will sometimes take the same form as in birds (C 6, C 7, and L 6). In the second column, we see the head-process (hp) above the primitive streak, and it is from this one that the embryo is evolved. This formation differs from that of the blastoderm in reptiles, a somewhat differently shaped neural groove (ng) taking its place. In the third column, an exactly corresponding neural groove, however, may be observed in birds (G 3). Below this groove, the formation of the notochord (*chorda dorsalis*) takes place, but this is of course not traceable in these surface cuts. The two folds at the sides of the neural groove swell more and more, constituting the neural folds and being the preformation of the brain and spinal cord. In the following columns of illustrations, these folds will be seen to approach each other, until they fuse, forming a tube through the median line of the embryo. The seventh column shows the development of three ventricles of the brain (b) in the upper part of this tube, and further, the sense organs, the eye (e) and the ear (er), appear. Previously, however, the so-called somites (s) have developed, originating from the mesoderm and appearing in Nos. 5, 6, and 7 as a series of square, light spots along the neural folds. It must be emphasized that these somites are preformations, not of vertebræ, but of some of the dorsal muscles. Several of the small pictures show how the amnion (a), a thin membranous sac investing the embryo, begins to form a fold above the top part of the embryo. It appears earlier in reptiles (L 5) than in birds (Ph 7), and in Ch 7 it covers almost the entire embryo with the exception of a small triangle below. C 6 shows the commencing cranial flexure, and C 7, figs. 59 and 60, the cervical flexure, so characteristic of reptile-embryos,

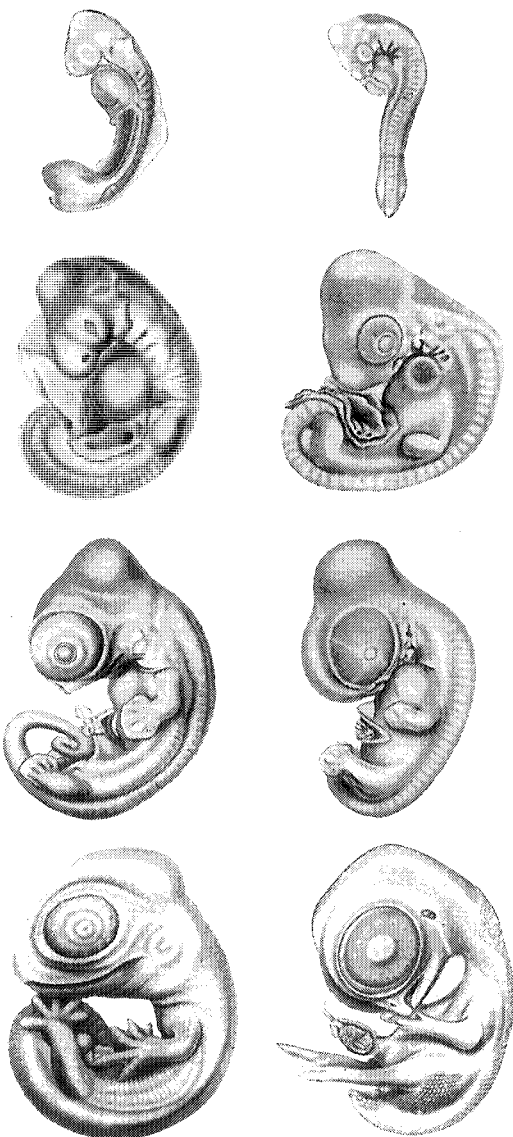
Fig. 59. Embryos of reptile and bird in four different stages of development. First vertical column: Lizard, second: Hen; after Keibel and Selenka. All figures are greatly enlarged.

birds, and mammals, in the later stages of their development.

The top column of fig. 59 shows nearly the same stages of development as the bottom one of fig. 58, but placed sideways in fig. 59. Presently also the limbs begin to appear as flat, rounded paws (Sp 7). They are a little more developed in the second column of figs. 59 and 60; here the tail, too, is plainly distinguishable. The development of the brain is accelerated; it looks like big bumps in the head of the embryo. The eye, too, comes out strongly; especially in birds and reptiles, it is enormously large; the nostrils and the internal ear also make their appearance. The heart (H) takes up considerable room; it looks as if the embryo were bending over this large heart so as to listen to its pulsations. I need not emphasize the striking resemblance between birds and reptiles in fig. 60; any one is able to see it for himself. The mutual difference between the two reptiles is almost greater than that subsisting between these and the birds.

In order better to illustrate the difference between the appearance of the full-grown animals, compared with the striking similarity between their embryos, I have in fig. 61 given a view of the heads of both. Words will here be found superfluous; the picture speaks for itself.

In the following front-views of heads (fig. 62), the brain and the eyes are the most prominent parts. I have here placed side by side the embryo-heads of Turtle and Hen at two different stages of development. The striking points of conformity are apparent. The arrangement of eyes and nostrils, oral orifice,



upper and lower jaws, is nearly alike in both; they seem to be as closely related to each other as two species within the same order.

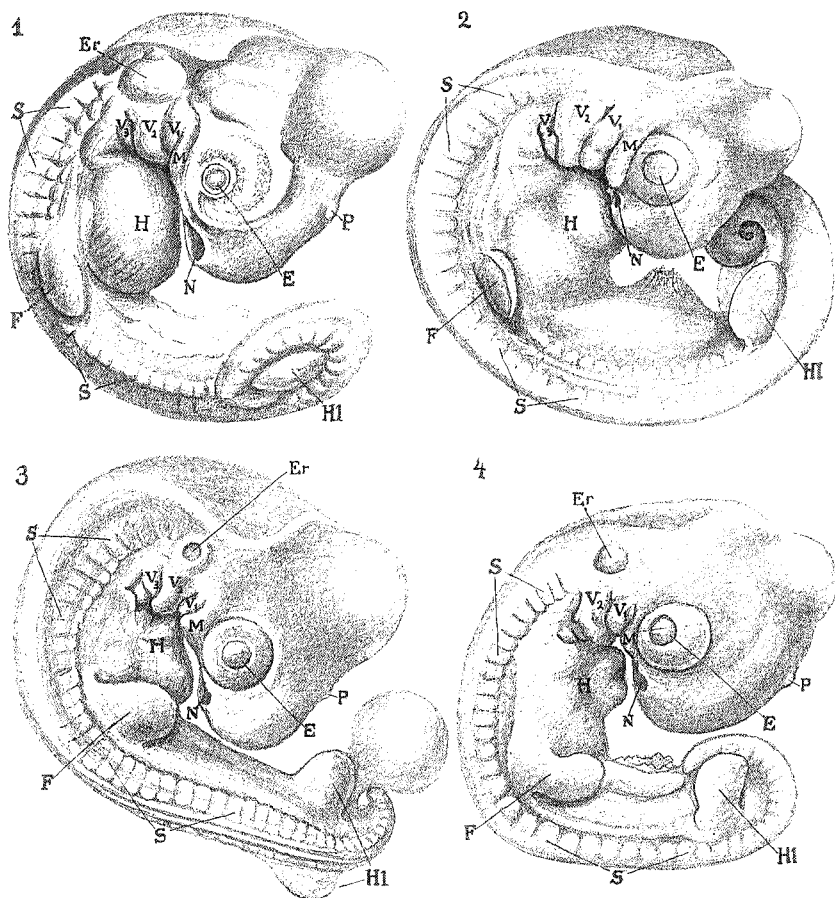


Fig. 60. Embryos of 1 Tuatera (*Sphenodon*), 2 Crocodile, 3 Hen, 4 Tropic-bird (*Phaethon*); 1 and 4 after Schauinsland, 2 after Voeltzkow, 3 after Duval. E eye, Er ear, F fore limb, H heart, Hl hind limb, M maxilla, N nostril, P pineal gland (see fig. 87, pg), S somites, V visceral arches.

The second series (fig. 63) represents a later stage of embryonic development, but in these heads, too, the resemblance is striking. The visceral pouches, plainly traceable in fig. 62, have disappeared, and the lower jaw has commenced to form. The expression of the different "faces" is very droll.

THE VISCERAL ARCHES AND THE SKELETON

It does not come within the scope of this work to follow up the development of each organ of the embryo; but we do find some exceedingly interesting facts, throwing a strong light on the kinship and origin of the vertebrates. For the elucidation of same we must learn some particulars.

Everybody knows that the fishes breathe by means of gills, i. e. that the renovation of the blood does not take place in lungs, but through the fine capillary network of the gills, which are fastened to cartilaginous or bony visceral arches, between which there are clefts for the water to pass through on its way from the mouth, thus oxidizing the gills. Now we meet with the peculiarity that all vertebrates have such visceral arches, even if after

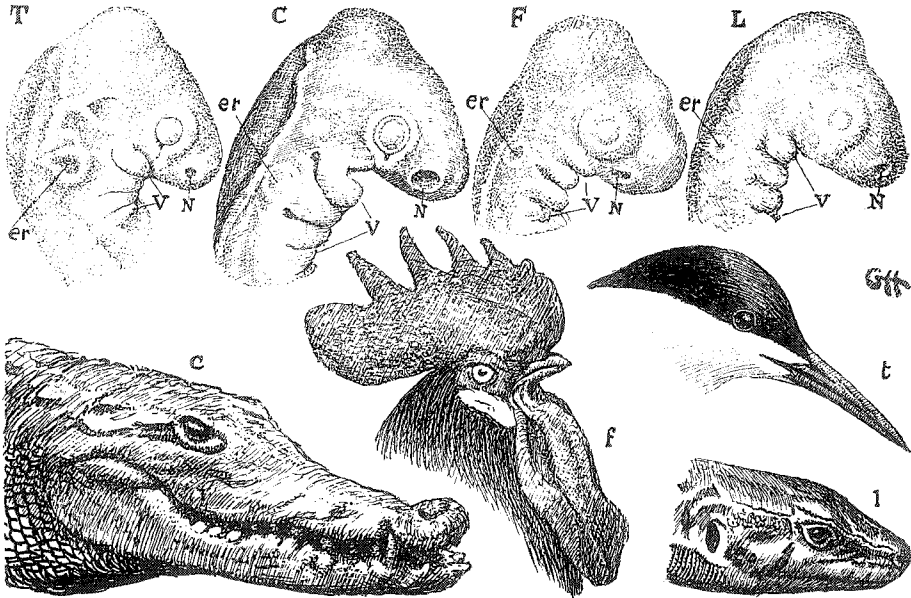


Fig. 61. Heads of embryos of C Crocodile, F Common Fowl, L Lizard, T Tern; C after Voeltzkow, G after Duval and Keibel, L and S after Schauinsland. N nostril, V visceral arches, er ear; c, f, l, and t heads of the adult animals.

birth they breathe by means of lungs only. In some of the illustrations above (figs. 59, 60, 61, and 62) we have already seen these visceral arches. They produce no gills, it is true, but of the five intermediate pouches found in reptiles, at least three become perforated (van Bemmelen, 7), and of the four pouches in birds, too, the three first break through, forming visceral clefts, the third one, however, for a few hours only (Verdun, 8). The visceral arches are really quite homologous with the gill-arches of fishes.

Fig. 64 shows this very plainly, for we can here, in the first place, compare the appearance of a fish-embryo (T) with the corresponding stage of development in a bird (Ha). The position of the visceral arches proves to be exactly alike in both cases. This might be a mere coincidence, even though the correspondency be very striking, but the three following cuts (G, Ac, and Ga) will show that their outer resemblance is not accidental. Here we see a part of a Hen-embryo, viewed as a transparent object, so that the inner organs become visible. Like the fish, its heart is as far up as the throat, while the

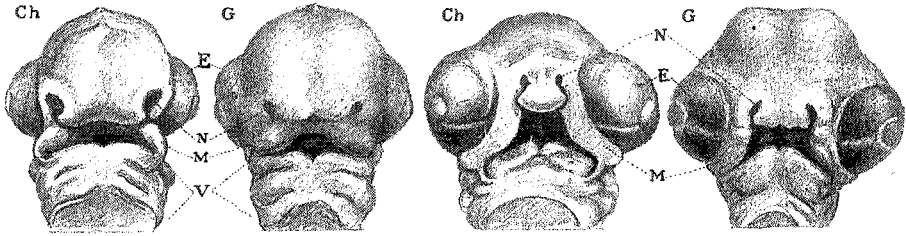


Fig. 62. Heads of embryos. Two different stages of development of Ch Turtle (*Chelonia*) after Voeltzkow and G. Hen (*Gallus*) after Lillie and Keibel; E eye, M upper jaw, N nostril, V visceral arches.

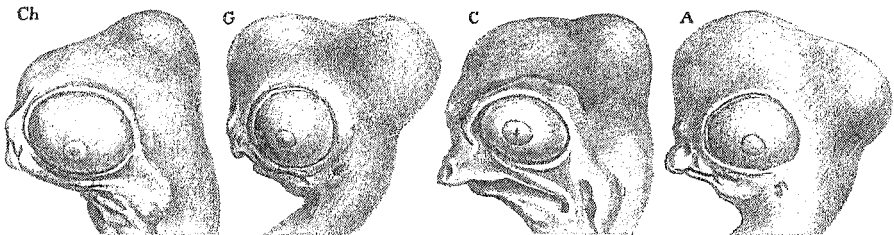
heart of the adult bird is down in the chest. And from the heart proceed the blood-vessels, one through each of the visceral arches, just as in fishes (Ga) and fish-embryos (Ac), which goes to prove that the visceral arches are exactly homomorphous in birds and fishes. In all vertebrates, such six blood-vessels (aortic arches) pass through the visceral arches on either side; in reptiles, only the third and fourth are persisting; in birds, the third and the right half of the fourth.

In Part I, we have already seen the close resemblance of a primitive bird's skull to that of a reptile, and hence it is sufficient to quote R. Lillie (9) about their embryos: "The embryonic bird's skull is characterized by a wealth of distinct bones that is absolutely reptilian; but in the course of development these fuse together".

The base of the spinal column is formed in the same way in all vertebrates, both ontogenetically and phylogenetically. It is a compact cellular rod called the notochord (*chorda dorsalis*). It is situate just below the medullary tube, and above the aorta and the intestinal tube. From the perichordal sheaths originate the substance of cartilage and bone which afterwards becomes the braincase and the vertebral column.

Most fishes retain this notochord also when grown up; it is then compressed in the middle of each of the biconcave and hour-glass-shaped vertebræ, expanding between these, thus assuming the appearance of a string of pearls running through the vertebral column. Although this notochord is useless as a supporting organ in reptiles and birds, it is always preformed in their embryos, and its close resemblance in the two classes is very great (Schauinsland).

Fig. 63. Heads of embryos in a later stage of development than fig. 62. Ch Turtle, and C Crocodile after Voeltzkow, A Duck after Keibel, G Hen after Duval.



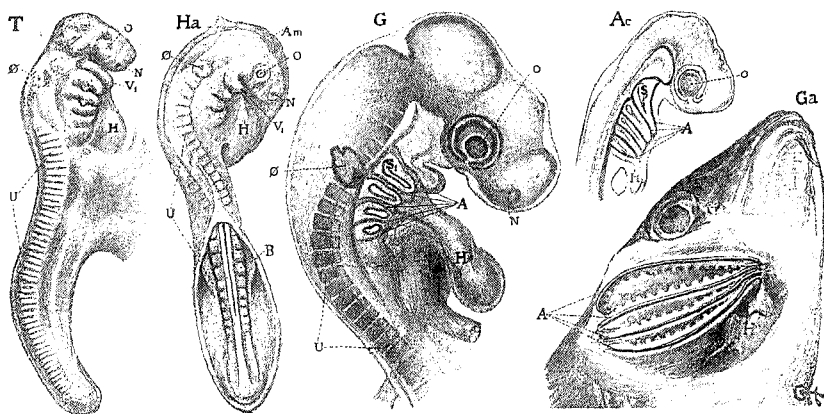


Fig. 64. T Embryo of Electric Ray after Ziegler, Ha embryo of Sooty Tern after Schauinsland, both in reflected light, G fore-part of a Hen-embryo after Duval, Ac forepart of a Shark-embryo (schematic) after Hochstetter both viewed as transparent objects, Ga head of a Cod (*Gadus*) whose gill-cover and gills are cut away, so that the heart and the blood-vessels running along the gill-arches are seen. A aortic arches, Am amnion, B hind-limb, H heart, N narial groove, O eye, S1 first visceral cleft, U somites, V1 first visceral arch, Ø ear.

The development of the vertebral column, too, is — on the whole — homologous in birds and reptiles, although the most heterogeneous shapes of vertebræ (procoelous, opistocoelous, and biconcave) are found in the latter class, while birds of the present day have vertebræ of a saddle-shaped, articular surface; the vertebræ of the Penguins, however, are opistocoelous. *Archaeornis* and *Ichthyornis* had biconcave vertebræ. Amongst existing reptiles, it is chiefly the Geckos that have biconcave vertebræ, and these reptiles retain the notochord all through life; but this shape of vertebræ is found in a number of extinct reptiles, e. g. Dinosaurs and the Parasuchians. It is, consequently, a very significant feature that biconcave vertebræ are found in bird-embryos, a fact fully illustrated in fig. 65.

A great many of the other vertebræ in birds are separate only while embryonic, and in the lumbar-region, the symphysis is usually complete. The bird-embryo, like the reptile, has but two pelvic vertebræ, and the great number found in the adult bird is due to an increase from the adjoining regions. When, therefore, we are surprised to find 20—21 caudal vertebræ in the *Archaeornis*, we must note that it has scarcely more than 4 pelvic vertebræ (*os sacrum*). A great number of caudal vertebræ, which are entirely separate in the bird-embryo, be it noted, are subsequently joined to the pelvis, forming a part of the sacrum, while others at the end of the tail grow together, forming the pygostyle. In *Hesperornis* and all Struthious

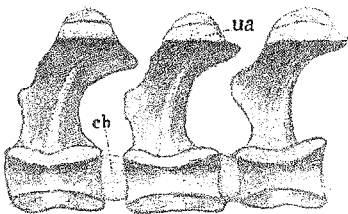


Fig. 65. The right side of three bisected vertebræ of the trunk of an 8-day chick after Schauinsland; ch notochord (*chorda dorsalis*) which runs continuously through the centra of the vertebræ; ua upper vertebral arch.

birds, there are as yet 12 separate caudal vertebræ, in the Swan-embryo 13 separate caudal vertebræ, and one more characteristic feature may here be mentioned, viz. that the preformation of the notochord (*chorda dorsalis*) in the tail of the bird-embryo is too long (Gadow, 10), and from this fact alone we may conclude that the original arrangement must have been like that of the reptiles; the same thing we learn from the tail of the *Archaeornis*.

The ribs originate from the vertebræ, and their development runs parallel in the two classes. Birds as well as reptiles (except the tortoises), in contradistinction to the mammals, have cervical ribs. All recent birds, with the exception of the Screamers (*Palamedeidae*), have uncinæ processes on their thoracic ribs; amongst the reptiles, it is chiefly the crocodiles and the Tuatera (*Sphenodon*) that have these processes fully developed. The uncinæ processes of the Tuatera, according to Schauinsland (6), are cartilaginous in their incipient stages, and appear later than the rib-cartilages themselves, from which they also are distinguishable by smaller cell-nuclei. The uncinæ process, during the entire life of the animal, remains separate from the ribs and never fuse with same; nor does any ossification, in the proper sense, take place, but only a calcination (fig. 66). The same thing holds true of the uncinæ processes of the crocodiles. In birds, on the contrary, these processes turn out differently. Just as in reptiles, they begin as cartilage and appear rather late (in the case of a Hen-embryo, on the 12th day). But later on, they ossify and generally grow together with the ribs themselves. Sometimes, however, this conjoining may fail to appear, as far as some of the ribs are concerned, and in the Kiwi (*Apteryx*) it does not appear at all. In the Crested Penguin (*Eudyptes chrysocoma*), and probably in the other penguins, too, the uncinæ processes remain cartilaginous during the entire life of the animal, and thus retain their reptilian character. The uncinæ processes of the ribs of *Hesperornis* were ossified, but not fused on to the ribs. Judging from this, we run no great risk in supposing that the ribs of *Archaeornis* actually had uncinæ processes, but that these were cartilaginous, hence not preserved in the fossil, as already indicated in Part I. In fig. 68, 4 we see a rib with uncinæ process of an extinct reptile.

The breast-bone is a product of the ribs. Fig. 67 shows that development is homologous in reptiles and birds. Some distal ends of the thoracic ribs fuse, forming a membranous expansion on either side of the median line. These two expansions will gradually approach each other, until they merge into a breast-bone plate. In reptiles, this plate remains cartilaginous all through life; no thorough ossification takes place, only a depositing of calcareous salts. But in birds, the power of flight requires a strong insertion-area for muscles, hence the ossifying process is thorough, issuing from centres of ossification on either side of the median line. To this we must ascribe the cause of the anomaly, sometimes found in birds, that the sternal keel is bifold, and were it not for the formation of the sternum from two lateral halves, the peculiar arrangement of the windpipe (*trachea*), in some birds, would be quite inexplicable to us. Every ornithologist, of course, knows that the very long

windpipe of the crane and of several swans must make more than one turn within the keel in order to get room enough. It is very characteristic and significant that the sternum of birds, which in the adult bird does not in the slightest degree resemble that of the reptiles, is thoroughly reptilian during the embryonic stages.

Several of the illustrations of fig. 67 show the preformation of a membrane bone called episternum or interclavicle. It connects the clavicle with the sternum, and is found in several extinct reptiles (*Cotylosauria*, *Pecylosauria*,

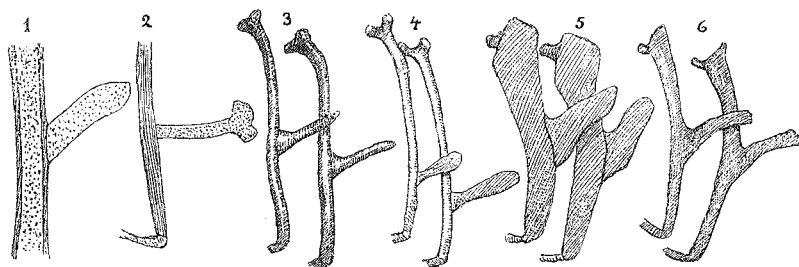


Fig. 66. 1 Longitudinal section through a piece of a rib with uncinate process of the embryo of Tuatera (*Sphenodon*); the ossification has commenced, the external bony tissue is seen, after Schaudinsland. 2 Piece of a rib with cartilaginous uncinate process of a nearly hatched embryo of Common Guillemot (*Uria troile*) after Parker; two ribs with uncinate processes of 3 adult Tuatera, 4 *Hesperornis*, 5 Kiwi (*Apteryx*) and 6 Flamingo.

Pseudosuchia (fig. 68, 1)) and several recent ones (*Lacertilia*, *Rhynchocephalia*, *Crocodylia*), but is wanting in tortoises and snakes, apparently also in birds.

In the embryo of the Hoatzin (*Opisthocomus cristatus*), Parker (11) has found an interclavicle situated exactly like the episternum of the reptile, because it "binds the furcula to the lower face of the sternum as in the Lizard" (fig. 67, 8 ic). The very fact that the clavicle of birds extends to the upper end of the sternal keel, is a proof of their conformity to the reptiles, for this part is exactly homologous with the episternum of the reptiles. Goette (12), who has most closely examined the development of the shoulder-girdle and the breast-bone of vertebrate embryos, says, in referring to the clavicle of the bird-embryo, as follows: "The preformation of the clavicle in each half of the shoulder-girdle contains only in its lateral part the clavicle proper, its median continuation at an early stage fastening on the median margin of the sternal half, and forming the episternal apparatus", see fig. 68, 3 and 69, 4. And further: "The median lamella, which constitutes the merging of the lateral halves, is now, as a matter of fact, in common with the entire Crista sterni, both as to its origin and relations, homologous with the episternum of the Saurians". How close the resemblance is between the bird-embryos and extinct reptiles, comes out by comparing Nos. 1 and 3 in fig. 68.

The preformations of the scapula, coracoid, and clavicle seem to be alike in the two classes. The scapula and coracoid ossify in perichondral fashion from independent centres of chondrification. The clavicle, on the other hand, never shows any trace of cartilage formations in birds, either in early or

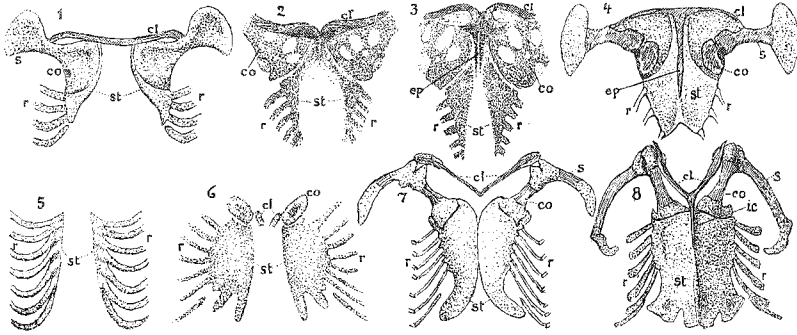


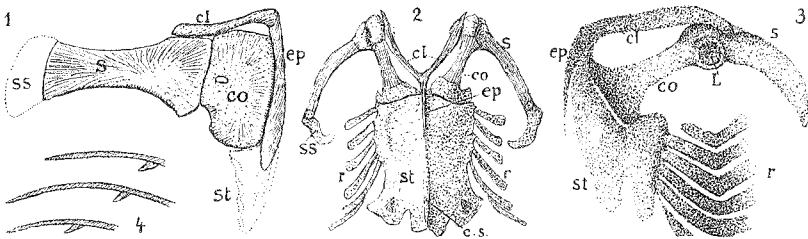
Fig. 67. The upper column shows different stages of development of the breast-bone in embryos of reptiles; 1 and 4 Tuatera (*Sphenodon*) after Schauinsland, 2 and 3 Lizard (*Cnemidophorus*) after Goette; the lower column the same in embryos of birds, 5 and 6 Hen after Lindsay, 7 Lapwing after Parker, 8 Hoatzin (*Opisthocomus*) after Parker; cl clavicle, co coracoid, ep episternum, ic interclavicle, r ribs, s scapula, st sternum.

more advanced stages, but ossifies direct from the membrane (Lillie, 9). The same thing holds good of reptiles, in which, amongst the various elements of the shoulder-girdle, the clavicles are the first to show ossification. In birds, the clavicle is the first centre of ossification in the body, and the bony deposits begin on both sides, approaching the mid-ventral line and fusing there, thus forming the furcula or wish-bone (9). *Hesperornis* (fig. 69, 7) had as yet distinctly separate clavicles, and as late as in the Lower Miocene, we may still find the same (fig. 69, 8). Thus we see ontogeny recapitulating phylogeny. In some recent birds, the clavicles are not fused at the adult stage.

In the embryo of the Hoatzin, Parker has found "the supra-scapula segmented from the scapula, a character as unsuspected as it is instructive" (11). That this is a reptilian feature, we shall find by comparing Nos. 1 and 2 of fig. 68.

In a four days old Hen-embryo, Goette (12) found that the clavicle, across the joint was attached to the shoulder-blade (fig. 68, 3). Moreover, fig. 69, 1, 2, 3, and 5 illustrate the same thing. As mentioned in Part I, this is a strong

Fig. 68. 1 Right half of the shoulder-girdle and breast-bone of the Pseudosuchian *Euparkeria capensis* after R. Broom, 2 breast-bone and shoulder-girdle of a Hoatzin-embryo (*Opisthocomus*) after Parker, 3 left half of the shoulder-girdle and breast-bone of a four days old Hen-embryo after Goette; cl clavicle, co coracoid, c. s. carina sterni, ep episternum, r rib, s scapula, ss suprascapula, st sternum; 4 three ribs with uncinate processes of *Euparkeria capensis* after Broom.



reptilian resemblance (cf. fig. 68, 1), and there we learned that in the two Jurassic birds, the scapula had a hollow for articulation with the clavicle. The same thing we find in *Apatornis* from the Cretaceous epoch. Marsh states in "Odontornithes" p. 147 about the clavicle: "It presents no face for articulation with the coracoid, but tapers to a flattened point at the top, where it is adapted for attachment to the acromial process of the scapula". This also shows how ontogeny repeats phylogeny.

Several embryologic investigations of the fore-limb have been made, but none sufficiently thorough to show the development of particulars from be-

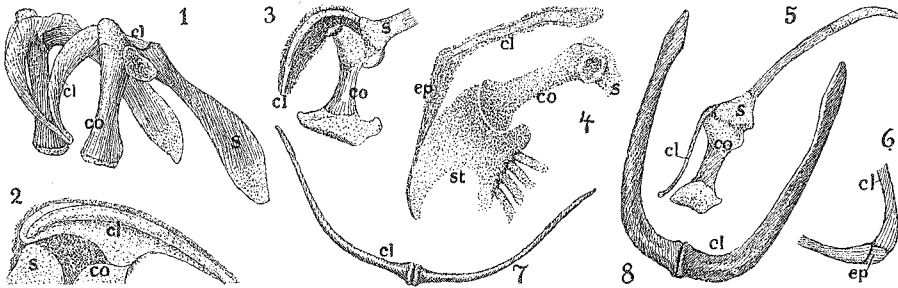


Fig. 69. Parts of the shoulder-girdle in different birds to show the connections of the clavicles mutually, to the episternum and to the scapula. 1 and 6 large squabs of Penguin (*Eudyptes*). 2 embryo of Lapwing, 3 embryo of Common Guillemot (*Uria troile*), 4 five days Hen-embryo after Goette, 5 embryo of Moor-Hen (*Gallinula chloropus*), 7 *Hesperornis* after Marsh, 8 *Palæolodus ambiguus* from the Lower Miocene after Milne-Edwards; 1, 2, 3, 5 and 6 after Parker; cl clavicle, co coracoid, ep episternum, s scapula, st sternum.

ginning to end, so they are of comparatively little value. In reptiles appears a dermal thickening, swelling into a fold on the limb-bud (Peter 13); in subsequent stages, this fold disappears again entirely. It is most distinct in the fore-limb of the Crocodile-embryo (F) as shown in fig. 60, 2. The limb-buds of the bird-embryo show an exactly similar fold, but same disappears still earlier. Later on, the main divisions of the limbs begin to appear, and at the same time the commencement of the skeleton will be traceable in transparent objects. If the adult animal has less than five digits developed, indications of the wanting ones may be found in the embryo, and these may either from the very beginning be homologous to the remaining ones, or they may appear later on and soon again disappear. Very often, however, there happens to be no trace of wanting digits. It is like a transitory reminiscence of the past.

But in this connection it is chiefly the preformation of the hand-skeleton that is of interest to us, and fig. 70 represents what Leighton (14) has found in the Tern (*Sterna wilsoni*). In the spatulate extremity of the fore-limb, we see the skeletal preformations as four digital rays (fig. 70, 1). One of these rays disappears again nearly altogether; Leighton calls this one the fifth; the other three he calls the second, third, and fourth. Why so? Let me quote his own words: "We are then left to choose between the formula I, II, and III, and II, III, and IV, and though the apparent weight of authority is in the

other direction, I am strongly inclined towards the second alternative, for the following reasons: First comes the law of digital reduction advocated by Morse, by which in other groups digit I is first to disappear and then V. Further,

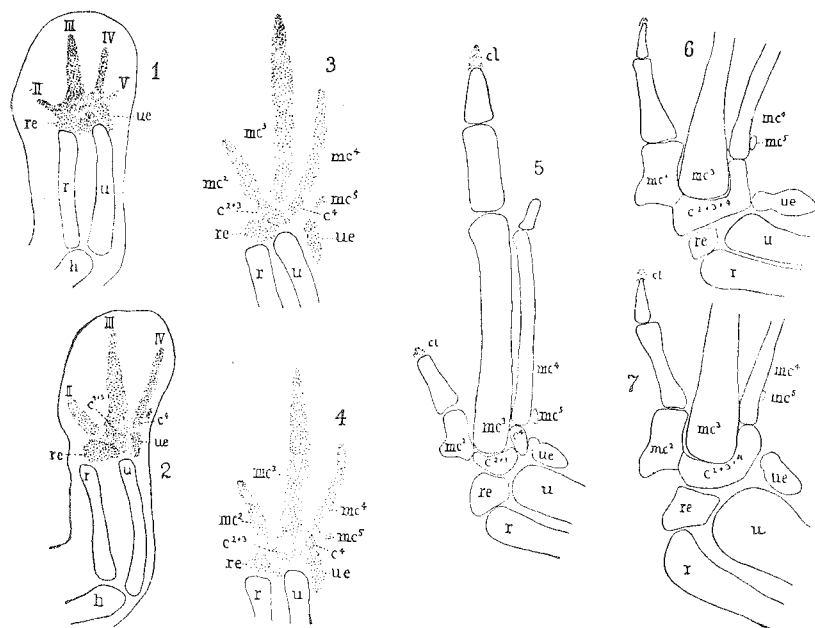


Fig. 70. 1—7 Slightly reduced reproduction of Leighton's original drawings of the development of the hand in the embryo of *Sterna wilsoni*; the letterings are Leighton's: c carpalia, cl preformation of claw, h humerus, mc metacarpals, r radius, re radiale, u ulna, ue ulnare, II—V preformations of fingers.

when further reduction occurs in birds as in *Apteryx* and the Cassowaries, the reduction has occurred on both sides of the persisting digit which, according to my nomenclature, would be digit III. This implies a symmetrical reduction, the other view involves the disappearance of digits I, III, IV, and V, a condition, so far as I am aware, without parallel".

Then he refers to the *Archaeornis siemensii* in support of his designation of the digits, saying: "Hurst points out that the position of the feathers is such that they could not have been borne on these digits as in ordinary birds, but that there must be at least one digit buried beneath the feathers". This falls short of being a convincing proof. In the fossil of *Archaeornis*, no "feathers" are preserved, only impressions of these, and nothing is "buried" beneath; both hands are in a state of splendid preservation, and had no fourth finger.

Leighton proceeds with similar "proofs" and says: "In regard to the first (I, II, and III) Hurst remarks, it 'is in no case, so far as I am aware, supported by any evidence whatever'."

It is a disappointment to read Leighton's article, for in such a first hand embryologic work, a lucid and convincing demonstration, based on the preparations themselves, would naturally be expected. Instead we get nothing

but some hazy assertions from other authors, who do not even seem to know what they are writing about, and by no means a logical argumentation. What he says about the *Apteryx*, moreover, is but circular reasoning, for he actually makes use of his own unproved digital figures by way of antecedent, on the basis of which he deducts the desired conclusion. The last quotation from Hurst is sufficiently refuted by fig. 19.

Leighton's own illustrations disprove his statements. We need only compare his mc2 and mc3 in fig. 70 with mc.1 and mc.2 of *Ornitholestes* in fig. 19 to see the striking resemblance. This shortened first metacarpal and elongated second metacarpal in *Ornitholestes* are evidently identical with those in the embryo of *Sterna*.

Mehnert's lengthy paper (15), too, contains mostly ordinary comments on embryonic development. He has examined the skeletal preformations of the limbs in the Tortoise and the Ostrich and describes same. In order to explain the bird's wing, we should expect that Mehnert by illustrations would show us a very abundant material for investigation at the different stages of development. But this he entirely fails to do; his only illustration is the one reproduced in fig. 71. It very nearly corresponds with Leighton's No. 3 in fig. 70, but the distal carpals of the Ostrich-wing is represented as one cartilaginous part (Cpd). The illustration reproduces a longitudinal section through the hand. Ulnare is but superficially hit, says Mehnert; as a matter of fact, it has nearly the same size as radiale. As the section, moreover, is taken through a part only of the outmost metacarpal cartilage (fig. 71, 4), the illustration is but little instructive. Mehnert has no difficulty in pointing out the digits (the metacarpal cartilages). With great certainty he designates them 1, 2, 3, 4, and he has no doubt that the peculiar excrescence from the second metacarpal cartilage is the preformation of the first digit. He does not even mention whether he has observed the disappearance of this excrescence or not, but only gives vent to the following statement: "From the ontogeny of the Ostrich-wing we learn that the tridactyl hand originates from the pentadactyl by the disappearance of the first and fifth rays. The persistent digits, then, are 2, 3, and 4, and the longest digit of the wing is not, as hitherto supposed by most authors, the second, but the third ray".

This view of Mehnert's, based on so slight evidences, in fact mere hypotheses, does not carry conviction. His interpretation of the metacarpals is

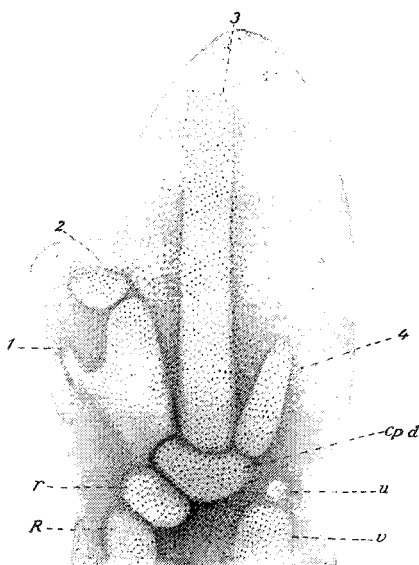


Fig. 71. Hand of a 16 days old embryo of Ostrich; direct reproduction from Mehnert's original and with his lettering; cp d distal carpals, R radius, r radiale, V ulna, u ulnare, 1, 2, 3, and 4 rays of fingers (preformation of metacarpals).

quite arbitrary, and the first broad one with its process, called 1, reminds one of the somewhat twisted form of the first metacarpal in *Archaeornis* (fig. 19, mc. 1). Other embryologists have designated the digits: the first, second, and third, but their statements are no better proved than those of Leighton and Mehnert.

The results gained from investigations of the embryo, as to the preformation of the digits on a bird's hand, are consequently unreliable, hence cannot alter the conclusion at which we arrived in Part I, when comparing the hand of

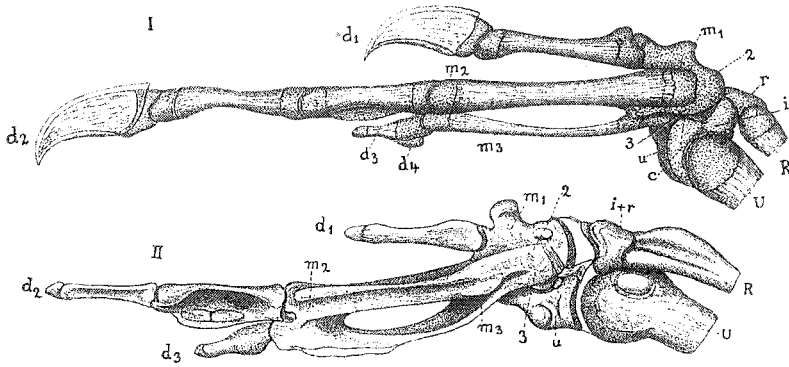


Fig. 72. I Left hand of Hoatzin-embryo, II left hand of adult Hoatzin after Parker; c centrale, d1—d4 first to fourth fingers, i intermedium, m1, m2, m3 the three metacarpals, R radius, r radiale, U ulna, u ulnare, 2, 3 distal carpals. I c. $\frac{1}{3}$ nat. size, II nat. size.

birds with that of extinct reptiles, viz. that the three digits of the former are first, second, and third, and that thus the development of the hand is homologous in the two classes.

The finest example of claw-bearing phalanges in bird-embryos (11) is the South-American Hoatzin (*Opisthocomus cristatus*). In fig. 72, the skeleton of the adult bird's hand is placed side by side of that of the embryo. The break subsisting between embryo and adult bird, is nearly as great as that between *Archaeornis* and the recent bird (fig. 17); in the embryo, it is true, the third digit is already stunted, but the first and second are long, greatly approximating those of the *Archaeornis*. The claw-phalanges are large and protruding, and in Part III, where we shall return to this peculiar bird, the cause of this fact will become evident (fig. 83—85).

In Part I, we have compared the carpus of the bird-embryo to that of the reptile (fig. 18), and found it exactly alike in both.

The development of the pelvis is very interesting. The preformation shows the same three elements in reptiles, birds, and mammals, arranged in the same form of three rays (fig. 73). That the preformation of the pubis at first points forward, but little by little turns backward, is a fact observed by all investigators. Fig. 73 will show this very distinctly. In No. 1, the preformation of the pubis points forward and downward, and the angle which it forms with the preformation of the hip-bone, is congruent with the corresponding

angle in the preformation of the reptile-pelvis (fig. 73 E) But while the pubis of the reptile retains its forward pointed position (fig. 73 C), it turns backward more and more in the bird-embryo, until its position is nearly horizontal. The pubis, then, is at first identical in reptiles and birds; the primary structure is alike, that is to say, they are homomorphous, and as their function is alike, too, they must certainly be considered homologous. I further wish to call attention to the fact that the hole (*foramen obturatorium*) in the pubis, constituting a passage for the *Nervus obturatorius* in the preformation of the bird-embryo (fig. 73, 1), is homologous with that of *Ornithosuchus* (fig. 13). *Archaeopteryx*, too, had an obturator foramen in the proximal end of the pubis (fig. 9). In the Chicken (fig. 73, 6), the acetabular part of the pubis keeps the same direction as the bone had in the embryo, while the tender, rod-like part is pointing backward. In Part I, the pectineal process (pr. pe) is minutely described as belonging to the ilium. The embryonic stages prove, with absolute certainty, that it develops as a cartilaginous outgrowth of the ilium (fig. 73, 5), and ossifies from the latter, not from an independent centre (Mehnert, 15).

By looking at figs. 74 and 75 we witness, so to speak, the development of the hind-limb from reptile to bird, and even though we were prepared to find something of that kind, we are struck with amazement to see five separate preformations of metatarsals (I—V) and the marked preformation of the fibula (Fi). Note that the fourth toe-ray (IV) in G1 is almost the longest, as often found in reptiles, and in *Archaeornis* we found a distinct fibulare and a fully developed fibula of the same length as the tibia (fig. 23, fi), — ontogeny is also here found to recapitulate phylogeny. The affinity between the preformations of tarsals in birds and reptiles, will appear from a comparison of G3 and E in fig. 74, and how these bones subsequently grow together, partly with the tibia, partly with the metatarsus, has already been alluded to in Part I, but this takes place at a comparatively late period, and in the case of the Chicken, the process is not yet finished (G5).

OTHER ORGANS

The preformation of the brain and spinal cord is, in general, practically alike in all vertebrate embryos, and so there is no special reason to dwell on it here. In Part III, a comparison of the brains in the various classes of vertebrates will be found, where also the organs of sense, the cuticular formations of scale and feather, and the organs of respiration will be dealt with.

A single fact, however, may already be mentioned in this connection. In fig. 58, we saw how the neural tube developed three ventricles at the upper end. In the hindmost of these ventricles, i. e. the one that somewhat later becomes the *medulla oblongata*, we find a number of projecting transverse folds, separating the walls of the neural tube into symmetrical sections. They are called the neuromeres, and several of these are connected with certain

nerve centres in the brain. Fig. 76 will give an idea of the striking resemblance between the two sets of neuromeres in reptile and bird respectively.

Moreover, the embryos of these Sauropsida show an amazing homogeneity in the development of most organs. According to Göppert (16), their mouths are, on the whole, formed like those of the gymnophiones. The development of the tongue is, in all essentials, parallel to that of the Lizard (*Lacerta*), says Kallius (17). The thyroid gland commences alike in both cases. In the development of the thymus, too, the difference between reptiles and birds

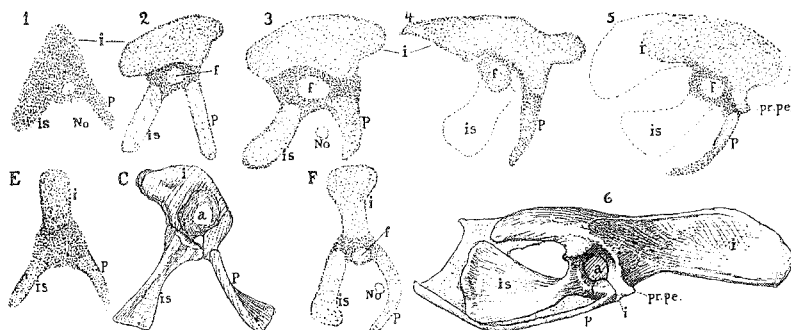


Fig. 73. 1—6 Development of the pelvis in embryos of 1 Slavonian Grebe (*Podiceps auritus*), 2 and 3 Black-headed Gull (*Larus ridibundus*), 4 and 5 Hen, 6 pelvis of a chick and C of a young Crocodile, E pelvis of embryo of Pond-Tortoise (*Emys orbicularis*) and F of Cat; a acetabulum, f head of femur, No nervus obturatorius, i ilium, is ischium, p pubis, pr. pe pectineal process. When the preformation of a bone is only indicated by a dotted outline it signifies that it is not hit by the cut. 1, 2, 3, E, C and F after Mehnert, 4 after A. Bunge, 5 after Mehnert compared with A. Johnson.

is entirely insignificant. In birds, the first formation of the intestinal canal is similar to that of the reptiles (Maurer, 18).

According to works by Hammar (19) and Brouha (20), the preformation of the liver in birds is in close conformity with the corresponding process in lizards, although its further development shows a more complicated structure. The development of the spleen, too, is alike in the two classes, but is also similar to that of the mammals. The same thing may be said of the kidneys.

About the development of the heart, we quote from Hochstetter (21), as follows: "The formation of the bird's heart shows, in many respects, a great affinity to the development of the reptile's heart. This is true, more particularly of the way in which the heart-tube at first curves (fig. 77, G1 and L1). Also the formation of the auricles runs parallel with the same process in reptiles, the expansion of the right auricle developing much later than the left one". And further: "The cavities of the heart of young Hen-embryos are similar to those of young Lizard-embryos". The interauricular septum "originates in quite the same way as in the case of the Lizard". In the environs of the heart, too, the formation is homologous, the development of the septum between the pericardium and the peritoneal cavity, in all essentials, running parallel in Lizard- and Hen-embryos (Hochstetter). The blood-vessel system is no exception: "The transformation to which the aortic arch is subject

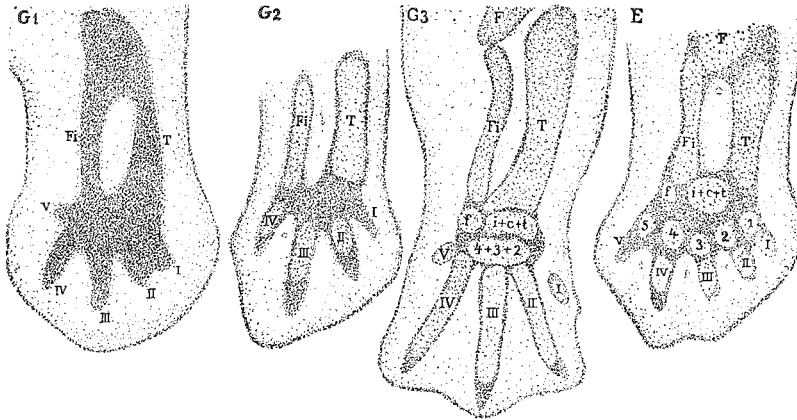
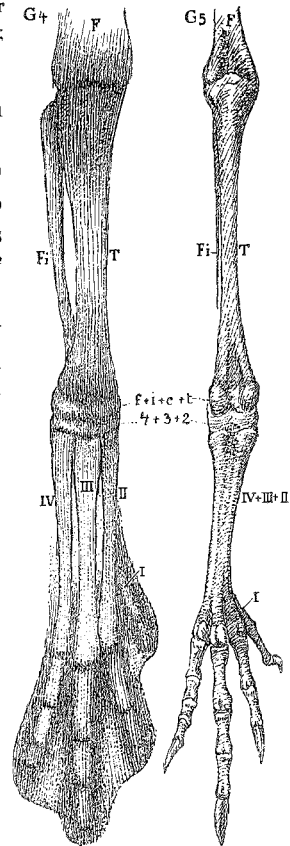


Fig. 74. G1, G2 and G3 longitudinal sections through the right hind-limb of a Hen-embryo in different stages of development; E the same of Pond-Tortoise; G1 and G3 after A. Johnson, G2 and E after Mehnert. F femur, Fi fibula, T tibia, c centrale, f fibulare, i intermedium, t tibiale, 1—5 distal tarsals, I—V preformations of metatarsals and toes.

Fig. 75. G4 right hind-limb of Hen-embryo on the ninth day after Gegenbaur, G5 hind-limb of a half-grown chick, nearly $\frac{1}{2}$ nat. size; Lettering as in fig. 74; I—IV metatarsals.



reminds one in many respects of those prevailing in turtles and crocodiles”.

The inner carotic artery (*arteria carotis interna*) presents striking points of resemblance. Referring to same, Hochstetter writes as follows: “In most birds the two inner carotic arteries run along the inside of the vertebral column in close contact for some distance, or, even as in crocodiles, they fuse together entirely for the same stretch, thus forming a bifurcated odd *arteria carotis subvertebralis*. This is seen in the Bittern (*Botaurus stellaris*), the Little Bittern (*Ardetta minuta*), a. o. One of these branches may disappear, the regular occurrence in the case of the crocodiles, and it may be either the left one, as in the Kiwi (*Apteryx*), the Grebe (*Podiceps*), a. o., or the right one, as in the Long-beaked Bustard (*Eupodotis*)”. The bracheal artery in birds, too, in its preformation, is similar to that of the reptiles; the same thing holds true of a great part of the venous system.

That there is a preformation of a tooth-ridge in bird-embryos (Gardener, 22; Röse, 23; Carlsson, 24) is presumably beyond a doubt, although too few embryos by far have as yet been examined. A glance at fig. 78 is sufficient to trace this tooth-ridge just inside the

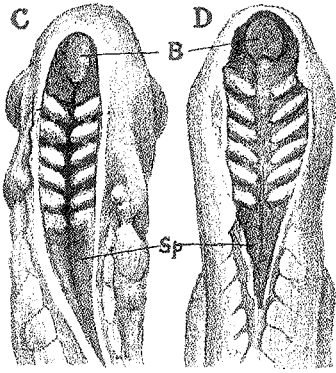


Fig. 76. Foremost part of embryo of C Green Turtle (*Chelone mydas*); D Albatross (*Diomedea*) both after Schauinsland; dorsal view; the thin cover of the hindmost ventricle of the brain is taken away so as to show the neuromeres, which are situate between the mid-brain (B) and the spinal cord (Sp).

margins of the jaws, and to show that it is homologous in reptiles and birds. Even in embryos of the edentate tortoises, preformations of the tooth-ridges have been traced. The transverse section of a lower jaw, shown in fig. 78, 5, is from a nearly hatched Ostrich-embryo, the tooth-ridge of which is evidently on the point of disappearing; — previous embryonic stages

of development have not been examined. Fig. 78, 4 shows the culmination of the tooth-ridge in Wilson's Tern, after which it gradually disappears.

Most reptiles have lips. The bird, in its full development, has none, owing to the jaws' being transformed into bills. Hence, it is a very significant fact that traces of same are found in their embryos (Gardener, Röse, fig. 78, 5 and 6). The same thing may be said of the Tortoise-embryo (fig. 78, 1).

It remains for us to mention the process on the upper jaw, by means of which the fully developed embryo breaks the egg-shell, and so from the close prison-cell of the egg emerges into the wide world. In Lizards (*Lacertilia*) and Snakes (*Ophidia*), it is a genuine dentin tooth (fig. 79, 2), fixed in the premaxillary, from which it points forward horizontally. Sluiter (25) has called attention to the fact that this "egg-tooth" was originally double (i. e. there was one in each premaxillary), and is still so found in some Geckos (fig. 79, 1), and in the Common Viper. In the bird-embryo, of course, there is nothing to correspond to this. But on the tip of the upper bill, it has a mammiform hard structure with pointed nipple, an accumulation of ectodermal cells (fig. 78, 6), by means of which it breaks the egg-shell. Such a shell-breaker we also find in the crocodiles (fig. 79, 4), and in the Tuatera. It is entirely homologous and analogous to that of the birds, its origin, development, use, and chemical composition being alike in the two classes. On account of its hardness and shiny white colour, we are

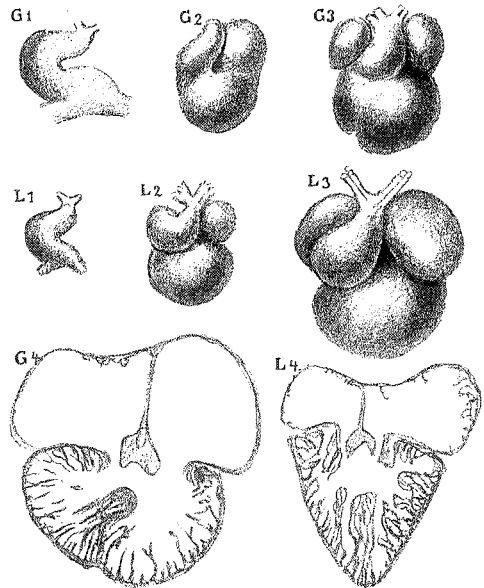


Fig. 77. Different stages of development of the heart in embryos of Hen, G1-4 after Greil and Hochstetter; G4 and L4 in longitudinal section.

apt to think that it contains calcareous salts, but by a careful chemical analysis under microscope, Röse (23) has proved that no calcareous salts at all are found in the shell-breaker. Sluiter (25), who also has analyzed it, is of the same opinion.

The shell-breaker of Turtles consists of a horn, rather broad at the base and sharp at the point, at the end of the nozle. In crocodiles, it is often two-horned at first, as shown in fig. 79, 6; but this double preformation is found in a few bird-embryos as well. The little young ones of birds, examined by myself, had all of them single shell-breakers; the Avocet (fig. 79, 9) only had

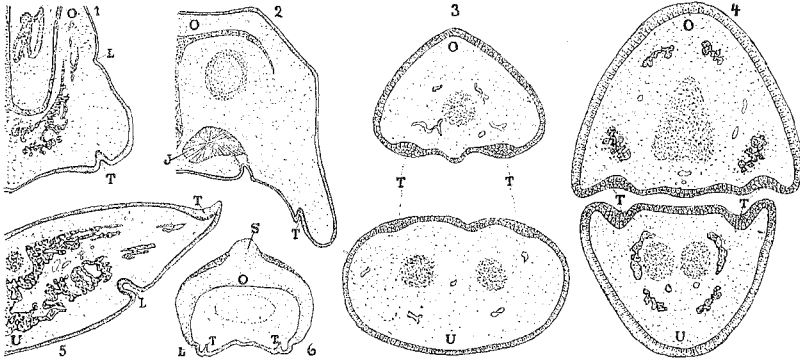


Fig. 78. Transverse section through the embryonic jaws of 1 Green Turtle, 2 Crocodile, 3 and 4 Tern, 5 Ostrich, 6 Hen; 1, 3, 4 and 5 after Röse, 2 after Sluiter, 6 after Gardiner. 1, 2 and 5 shows but a part of the section through the jaw; J preformation of Jacobson's-organ, L lip groove, O upper jaw, S shell-breaker, T tooth ridge, U lower jaw.

two flat off-shoots running backwards from the one point. In the ducks, the shell-breaker is found on the nail of the upper bill, in birds of prey and in owls, it is some distance from the point of the bill; the variety of shapes is but small. — In reptiles having an egg-tooth, no shell-breaker is found, and vice versa; one excludes the other. Either is cast off soon after hatching; a few young ones of birds, however, will retain the shell-breaker for nearly a couple of weeks. It has been generally believed that the egg-tooth was used for cutting the parchment-like egg-shell, while the shell-breaker was to break the calcareous part of the shell. But this does not hold true, for the eggs of the Geckos have a hard calcareous shell, while, on the other hand, those of the Turtles are parchment-like. Whether the origin of the shell-breaker is due to the affinity between reptiles and birds, I think it quite impossible to decide with any degree of certainty; it may just as well be due to convergence, a homologous adaptation through propagation by means of eggs. In the preceding pages we have found so many and amazing points of inner resemblance in the development of reptiles and birds, that it is almost refreshing for once to meet with a little difference, or rather a slight aberration in their close kinship.

As we have called attention to now and again, the structure of some organs in the embryo of birds bears a striking resemblance to the corresponding

organs in the Jurassic birds or in fossil reptiles. This agrees with the well-known fundamental law of biogenesis, formulated by Haeckel: The development of the individual, or ontogeny, is a brief recapitulation of the evolution of the species, or phylogeny.

It is a mistake to call this a law, because the special conditions prevailing in embryonic life make it impossible for the embryo to resemble a fossil animal in its entirety; there are also many other circumstances which obscure the results. But taking it only as a limited rule of repetition, we may, with proper caution, make use of it.

I have thus collected the following list of facts:

The vertebræ of bird-embryos pass through a stage of development in which they are biconcave. *Archaeornis* (26) and *Ichthyornis* had biconcave vertebræ.

The bird-embryo, just like the reptiles, had at first only 2 pelvic vertebræ fusing on to the sacrum, subsequently more of these appear. *Archaeornis* had 4.

The pygostyle at the end of the bird's tail consists in the embryo of 6 distinct preformations of vertebræ. The embryo has further 12—13 separate tail-vertebræ, consequently 19 in all; *Archaeornis* had 20—21.

The sternum of the bird-embryo commences as two lateral halves; in adult fossil reptiles, the same arrangement is found.

The bird's furcula, looking like an odd bone, is preformed in the embryo as two individual halves, separate in the mid-ventral line. *Hesperornis* had two distinctly separate clavicles.

In the embryo of birds, the clavicle has an attachment to the scapula. The same thing is to be found in birds from the Jurassic and Cretaceous periods.

In the embryo of the Hoatzin, the supra-scapula is separate from the scapula, as in fossil reptiles. — An interclavicle is also found in the same embryo, situated exactly like the episternum in fossil reptiles.

Seven carpals may be found as preformations in the bird-embryo, while the adult bird has only two. *Archaeornis* had six.

Four distinct preformations of metacarpals and digits may be found in the bird-embryo. *Archaeornis* had three digits and three separate metacarpals.

Frequently the number of phalanges in the three digits of the bird-embryo is 2—3—2, while the adult has 1—2—1. *Archaeornis* had 2—3—4.

Claws on the digits of bird-embryos are often found. *Archaeornis* had claws on all three digits.

In the Penguin-embryo, the skeleton of the fore-limb is at first developed somewhat like a bird's wing. Several separate carpals are preformed, so is the first metacarpal, which later on fuses altogether with the second. The wing-skeleton of fossil penguins approximates the embryonic wing of recent penguins.

The pubis in the bird-embryo is at first pointing forward, an arrangement found in fossil reptiles.

In its preformation in the bird-embryo, the fibula is just as long as the tibia, a structure also found in *Archaeornis* and fossil reptiles.

The tarsals of the bird-embryo are separate *inter se* and from the tibia and the metatarsus. This structure, as also the subsequent transformation, we find

in the Dinosaurs of the Trias and Cretaceous periods and in Archaeornis (26) as well.

The metatarsals are distinctly separate in the embryo, just as in the Jurassic birds and in the Coelurosaurs.

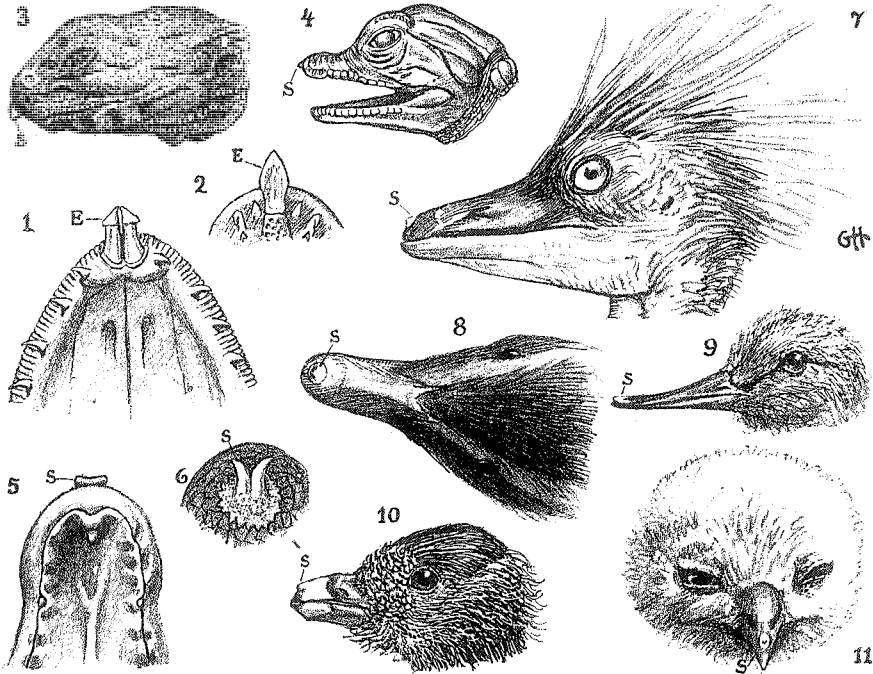


Fig. 79. 1 and 2 egg-tooth in reptiles, 3—11 shell-breaker in reptiles and birds. 1 Gecko just before hatching, upper jaw seen from below after Sluiter, 2 Lizard, upper jaw from below after Leydig, 3 Tuatara (*Sphenodon*) after Schauinsland, 4 Crocodile after Voeltzkow, 5 foremost part of upper jaw of same, seen from below, after Voeltzkow, 6 snout from above of Estuarine Crocodile (*C. porosus*) after Sluiter, 7 Heron (*Ardea*), 8 Eider-Duck (*Somateria*), 9 Avocet (*Recurvirostra*), 10 Common Coot (*Fulica*), 11 Snowy Owl (*Nyctea*). E egg-tooth, S shell-breaker.

The foot of the bird commences in the embryo as 4—5 rays. In the Ostrich, the preformation of 4 toes appear simultaneously. The development of the two, however, stops at an early stage, and the fully developed foot has only two toes.

In the embryo of the bird, a tooth-ridge appears in both upper and lower jaws. Fossil birds had teeth in their jaws.

The Jacobson's-organ (*organon vomero-nasale*), wanting in birds, is found in their embryos (F. Cohn, 27; fig. 78, 2 J), and this preformation is entirely homologous to that of the reptiles.

The cæca in birds differ considerably in their developments; in some birds they are very long, in others rudimental or entirely wanting. The preformation of the cæca in the bird-embryo is always well developed, even though the adult bird has no cæca at all (an inheritance from the reptiles, Gadow, 10).

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PART III

SOME ANATOMICAL AND BIOLOGICAL DATA

THE SUPRATEMPORAL FENESTRA

IN Part I, we have already compared the individual bones in the skeleton of the fossil birds and reptiles; and in Part II, the development of the skeleton of recent forms. The resemblance was so close that we hardly met with any differences at all. Hence, we need not compare the bones of modern birds and reptiles; only a temporal hole, found in the skull of a few birds, may be worth mentioning.

Several authors, e. g. F. v. Huene (1) and O. Abel (2), have called attention to the fact that the supratemporal vacuity is present in some recent birds. For some time past I used to be of the same opinion, considering it homologous with the supratemporal fenestra in reptiles, but only because, at the time, I was unable to procure the skull of a chicken of these Game birds, Cockatoos and Storks, for a more minute examination of the bones in question.

Now, however, I am able to say with tolerable certainty that this hole is a recent feature, and no relic from the past.

The supratemporal fenestra, in fossil reptiles, is always bounded by the parietal, which constitutes the inner margin, and the upper edge of the squamosal; further by the postorbital (fig. 80, 1), or the postfrontal (fig. 80, 2), or by both of these bones (fig. 80, 3); sometimes the frontal, too, enters the boundary line (fig. 80, 4 and 5).

The bone-framed hole, on the other hand, found behind the orbit in some Game birds: the Pheasant, the Quail, the Capercaille, and also at times in the Common Fowl, is bounded exclusively by the lower part of the squamosal and the alisphenoid (fig. 81, 4). Consequently, its character differs considerably from that of the supratemporal fenestra in reptiles.

The hole is not present in the skull of the young bird (fig. 81, 5), because the ossification does not set in until later on. This is also evidence against an inheritance.

While the supratemporal fossa of reptiles is best seen from above, and in many skulls not observable in lateral view, the case is entirely the reverse in birds, where the temporal hole is best seen from the side; and in order to draw it from above, as in fig. 80, 6, I have been obliged to tilt the skull a little, otherwise the opening could not be seen.

The alisphenoid in Theropodous Dinosaurs is described and illustrated by Ch. W. Gilmore (3) in *Antrodemus valens* (fig. 80, 8 and 9). "Superiorly it unites with the frontal and parietal, posteriorly, with the prootics", and exteriorly, with "the postfrontal postorbital complex". Its ventral process "laps along the sides of the basisphenoid". "On the posterior side the bone is notched by the

foramen ovale through which the trigeminal or fifth nerve makes its exit from the brain". It is of importance to note that the alisphenoid does not touch the squamosal at all. — In birds, the alisphenoid takes the greater share in forming the posterior wall of the orbit, and joins the frontal at this place, while laterally it joins the squamosal, which in most cases separates it from contact with the parietal (fig. 81). It is further joined by the basisphenoid; and the alisphenoid and the prootic (petrosal) enclose between them the foramen ovale, through which passes the third branch of the trigeminal nerve. According to these facts, there can hardly be any doubt that the alisphenoid in reptiles is homologous with the alisphenoid in birds.

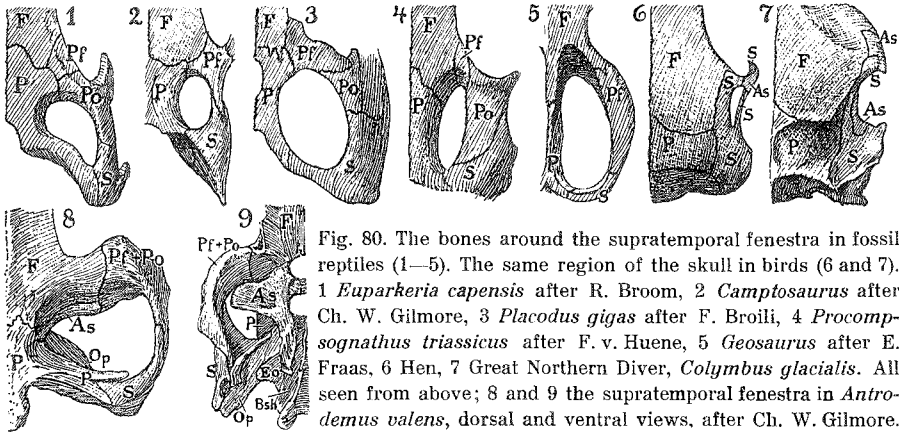


Fig. 80. The bones around the supratemporal fenestra in fossil reptiles (1—5). The same region of the skull in birds (6 and 7). 1 *Euparkeria capensis* after R. Broom, 2 *Camptosaurus* after Ch. W. Gilmore, 3 *Placodus gigas* after F. Broili, 4 *Procompsognathus triassicus* after F. v. Huene, 5 *Geosaurus* after E. Fraas, 6 Hen, 7 Great Northern Diver, *Colymbus glacialis*. All seen from above; 8 and 9 the supratemporal fenestra in *Antrodemus valens*, dorsal and ventral views, after Ch. W. Gilmore.

Lettering as in figs. 3 and 5.

From the drawings in figs. 80 and 81, it is not difficult to form an opinion as to the transformation of the temporal region, from reptile to bird. The braincase has expanded considerably, so that the supratemporal fenestra has gradually closed up; at the same time Pf and Po have disappeared, and the alisphenoid has thus joined the squamosal, an arrangement peculiar to the bird. From this it will also appear evident that we are not entitled to homologize the hole, recently formed, in the skull of some birds, with the supratemporal fenestra in fossil reptiles.

The temporal hole in the said Game birds is formed so as to be of support and protection to the temporal muscle, which originates from the inside of this hole, or rather channel, and inserts on the mandible (fig. 81, 6). The part of the squamosal which is above the quadrate, extends a long process in the direction of the muscle, and the upper part of the alisphenoid sends out a somewhat curved, vertical projection (fig. 81, 4 and 5) to fuse with this process. A strong ligament runs from the alisphenoid projection to the mandible, keeping the latter in position (fig. 81, 6).

In some Storks (fig. 81, 2), we find the hole framed exactly as in the Game birds, exclusively by S and As. I quote from P. Ch. Mitchell (3*), who, writing about the Jabiru (*Xenorhynchus*), describes the "postfrontal" process, and

says: "Close scrutiny seems to show that the frontal contributes a superficial splint-like factor, running down almost to the tip of the anterior face, and that the squamosal forms the greater portion of the lower and posterior part". "The spur of the squamosal from over the quadrate articulation is enormous and forms a powerful process, which runs downwards and forwards to meet

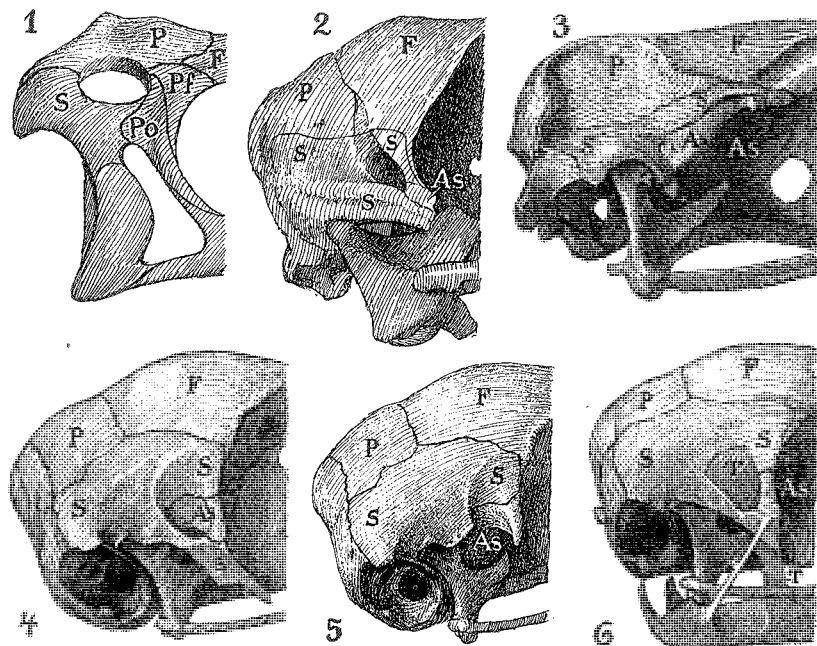


Fig. 81. Hind part of the skull of 1 *Aëtosaurus ferratus* after F. v. Huene, 2 Jabiru, *Xenorhynchus*, 3 Great Northern Diver, *Colymbus glacialis*, 4 adult Pheasant, 5 young, nearly full grown, Pheasant, 6 Hen; As alisphenoid, F frontal, P parietal, Pf postfrontal, Po postorbital, S squamosal, T temporal muscle.

and fuse with the tip of the postfrontal". My drawing shows how much the alisphenoid partakes in this process. — The hole in Marabous (*Leptoptilus*) is enclosed in a strong bony frame, but in other members of the family (*Ciconiidae*) the two processes do not meet.

The framing of the temporal hole in Cockatoos, too, is composed of the squamosal and alisphenoid only; in allied forms of parrots, there is no hole. R. W. Shufeldt (4) writes about a parrot: "The orbit is entirely surrounded by bone. This is effected in *Palaeornis docilis* by the infero-posteriorly extending process of the lachrymal bone uniformly curving backwards to touch, but not to fuse with, the anterior apex of the squamosal process". He further states that in the different species of *Ara* "posteriorly it completely fuses with the post-frontal process". The same is to be found in *Amazona leucocephala*, "but as it passes the apex of the squamosal process below, it develops a slight elevation on its lower edge, which is directed towards the apex of the squamosal process as though it were making an effort to reach it". In Cockatoos

this union is attained, and a large foramen is formed, which encloses the temporal muscle. We are here, so to speak, witness to the forming of the temporal hole once more; it is a recent formation, by no means to be parallelized with the fenestra temporalis superior of the reptiles.

The deep and broad groove in the temporal region of the Divers and some other aquatic birds (Penguins), also looks as if it might be a remnant of the supratemporal fossa in reptiles. It ends in a large excavation (fig. 80, 7), bounded anteriorly and posteriorly by a process, but the two bones, S and As, are exactly so placed (fig. 81, 3) as we have seen them in other birds, the squamosal sending out a long projection above the alisphenoid. In this instance, too, homomorphism is out of the question.

DIGITAL CLAWS AND RETARDATION OF PRIMARIES

If we did not know *Archaeopteryx* and *Archaeornis*, we should be unable to understand why so many birds have digital claws on their wings, in spite of the fact that these are exclusively used for flying. The claws are evidently a relic from the past, and they are a very common feature in the feathered world. Most frequently the first digit has a claw, less frequent is one on the second digit as well. This we see in the Ostrich (fig. 82), the Cassowary, and the Emeu, also at times in the Rhea and in the Kiwi, which latter has no first digit. Nestlings of many birds have claws on both first and second digits, e. g. Ducks and Geese, Kites, Terns, Avocets, Pratincoles, Godwits, and Coots, and in very many of these only the first digit has a claw.

Many adult birds, too, have a claw on their first digit. We may find it among Game birds, Ducks, Geese, and Swans, in which the claw often resembles a flat nail; further, among Vultures, Hawks, and Eagles, even in a few Perching birds. An obvious example presents our common Water-rail (*Rallus aquaticus*), whose digital claw is of a dark brown colour, while the length may vary in the different individuals; I have measured one nearly 7 mm long. It is closely invested by the feathers, running in the same direction, only the tip is bent a little towards the inside of the wing.

Many nestlings also make use of these digital claws in crawling about and in getting out of the nest, but it may suffice to describe the most striking and ancient-looking of these, that of the curious South American bird, the Hoatzin, *Opisthocomus cristatus*, an aberrant member of the Gallinaceous birds. Its nest is built in bushes, overhanging the water of streams, and soon after hatching, the young are capable of climbing about, with marvellous agility, on the surrounding branches, beak and wings being used as auxiliaries to locomotion, so as to make these young ones, at this stage, genuine quadrupeds. When pursued, they voluntarily throw themselves into the water, dive and swim under the surface, using both feet and wings as propellers. The adult bird possesses none of these accomplishments (5).

Fig. 83 shows a newly hatched nestling of Hoatzin; the shell-breaker on the upper beak is still conspicuous. It is covered with a loose down only, but

the primaries have already begun to sprout. The wing is of considerable length, the hand being particularly long in proportion to the forearm. Both the first and second digits have retained the claws from the embryonic stage (fig. 72), the first digit being, proportionally, of the same length as that of *Archaeornis*, and the second overhanging the distal primaries, both of them thus being well fitted for climbing. Their "finger-like" shape and the deep pigmentation of the claws are signs of their improvement, and the hollow of the claw faces the underside of the wing.

The proportions of the three bony parts of the fore-limb of this nestling, bear a close resemblance to those of *Archaeornis*; the hand of either is much longer than the arm and forearm; the proportions of the first and second digits also correspond. This is surely no mere coincidence, and in fig. 21 we have already compared the development of the primaries with that of *Archaeornis*, and called attention to the striking resemblance. That *Archaeornis*, therefore, has been able to climb the branches in nearly the same way as the Hoatzin-nestling, seems very probable indeed.



Fig. 82. Wing of Ostrich after C. W. Beebe.

W. P. Pycraft (6) has adverted to the retardation in the development of the distal primaries of this nestling, and fig. 85 illustrates the same remarkable feature. The remiges begin to sprout long before the feathers appear on the body, and their sequence of development is rather curious, for the proximal primaries on the margin of the hand, are the first to appear (fig. 85, II and fig. 83), then the secondaries, the wristward feathers first (fig. 85, III), and finally the most distal primaries at the tip of the second digit (fig. 84, II). No. 5 of the primaries is thus, proportionally, a well developed feather at the time when No. 10 has just begun to sprout.

The reason for this is not difficult to understand, for if all the primaries were growing at the same rate, the outermost ones would soon render the wing useless as a climbing organ, as they would impede the grasping power and the use of the claws. Not until the proximal primaries have formed a wing-area large enough to be used as a parachute, do the distal primaries start to grow, and from that time they develop rapidly. At the same time, the growth of the arm outstrips that of the hand, thus reverting the original proportions, the hand in the adult bird being shorter than the forearm (fig. 85, IV); the



Fig. 83. A Nestling of Hoatzin, *Opisthocomus cristatus*, B right wing of same, from the inside, photographed for this work by Dr. R. W. Shufeldt from specimens in the collection of the Brooklyn Institute Museum; nat. size, 1, 2, 3 first, second and third fingers.

claws disappear, and the first digit becomes shorter than the third one, which latter in the illustration appears on a level with the seventh primary. Nor does the second digit any longer protrude beyond the fold of skin in which the feather barrels are lodged; the bird has become a flying creature instead of a climbing one. Fig. 84 shows photographs illustrating this interesting feature in the development of the feathers; in the relatively large wing with half developed feathers, the claw-bearing finger-tips are still quite distinct.

This strange retardation in the growth of the distal primaries, is no isolated feature in the feathered world. In nestlings of Curassows, Common Fowl, Turkeys, and Megapodes, Pycraft (6) has found the proximal primaries, 1—7,

fairly well developed, while the three outermost quills, 8—10, at the same time appeared as nothing but down. This leaves the tip of the digit free as in the nestling Hoatzin, but the thumb and second finger do not display the thickened, sensitive lower surface seen in the latter, and the digital claws are present during their embryonic life only. Fig. 85, G illustrates the accelerated



Fig. 84. I Left wing of a nestling of Hoatzin, and II, the same of a young Hoatzin, both from the inside, photographed for this work by Dr. R. W. Shufeldt from specimens in the collection of the Brooklyn Institute Museum; both in natural size, 1, 2, 3 first, second, and third fingers.

development of the primaries on the metacarpals, 1—6, in proportion to those of the digits, 7—10; the hand is already shortened, but still longer than the forearm. A comparison with fig. 85, III will bring out the fact that the difference between the developed and the rudimentary primaries, is rather great in the chick compared to that of the Hoatzin, thus indicating that in the development of the wing for flying, life on the ground required a still greater acceleration than what was requisite for arboreal life.

This curious order in the development of the remiges would have been unintelligible but for our knowledge of the Hoatzin. Pycraft gives the following solution of our problem: "The wing of the nestling game birds is a survival

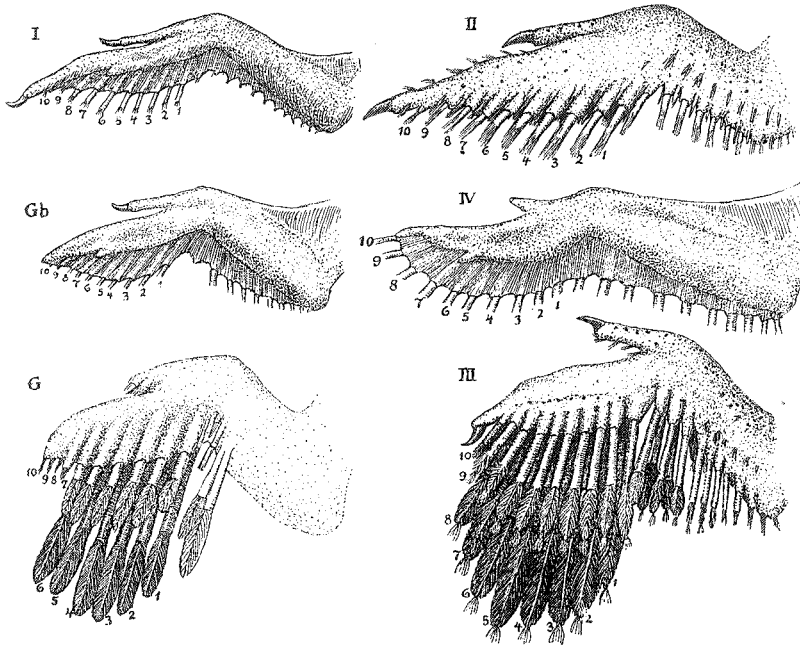


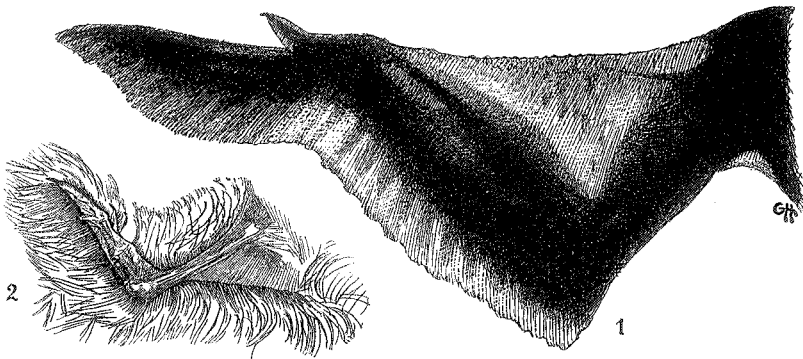
Fig. 85. I, II and III wing a nestling Hoatzin in different stages of development, I from the inside, II and III from the outside; IV wing of adult Hoatzin from the inside; Gb wing of a chick of the Jungle-fowl (*Gallus banciva*) and G, of a common chick, from the outside; after W. P. Pycraft.

The numbers indicate the primaries; in front of 7 is seen the tip of the third finger.

of an earlier phase of existence, when these birds, like the hoatzin, were reared in arboreal nurseries. This explanation alone can account for such a curious arrest in the development of the outer quills. It is a phase which is slowly being obliterated, as is shown by the fact that the nail-bearing joint of the second digit fails to survive the embryonic stage”.

Pycraft is no doubt right in this statement, but there is another curious

Fig. 86. 1 Right fore-limb of a Common fowl deprived of the feathers to show the patagium, drawn as a transparent object, bones, muscles, tendons and the like thus appearing as dark parts. 2 Right wing of young Ostrich (*Struthius danaoides* Shelly) from Kilima-ndjaro, drawn by Sir Harry Johnson.



feature in the wing of these nestlings, of which he offers no explanation. It is the retardation of the innermost secondaries, clearly discernible in fig. 85, G and III. This cannot be due to climbing, there must be another reason. Better developed feathers in this place would have made the wing-area more suitable for gliding through the air, and from the wanting feathers we may infer that something else was originally acting here as a parachute. Our nearest guess would be a patagium, extending from the arm along the side of the body. Such a fold of skin is the first to appear when the evolution of a "flying" mammal sets in, and therefore it does not seem unlikely that an incipient patagium was present in some forerunner of birds, in due time giving place to the fully developed wing of feathers. Consequently, the traces of this kind that we may expect to find in modern birds, are but small; nevertheless, fig. 86, 2 shows a still persisting patagium between the arm and the trunk of a young Ostrich. Of this we find but a small vestige in the Hen (fig. 86, 1), which has a postpatagium, running from the tip of the second digit to the elbow, and a prepatagium, extending between the wrist and the shoulder.

CEREBRUM AND CEREBELLUM

In this Part, we are more particularly to compare the most important of the organs, in reptiles and birds, which as a rule are not preserved in the fossils, and so we commence with the brain, of the main features of which fig. 87 gives a general view. The foremost large part of the brain, the cerebrum (C), is divided into two symmetrical hemispheres by a deep longitudinal fissure. In sections, it proves to be composed of a cortical mantle or pallium (P), and a lower part containing the basal ganglia (G). The surface of the hemispheres is, in birds and reptiles, quite smooth; it exhibits none of the convolutions peculiar to the brain of the higher mammals (fig. 87, 7). In some orders of birds, however, there is a single, very slight furrow, indicated in fig. 88, 8 at the end of the line running from C, and also in figs. 26 and 30. The anterior end of the brain is composed of the olfactory lobes (ol), which are strongly developed in reptiles. Behind the cerebrum are the globular optic lobes (op), not distinguishable in side view of the mammalian brain (fig. 87, 7), in the case of which they are enclosed by the cerebrum.

A singular projection from the midbrain is the epiphysis or pineal gland (pg of fig. 87 and 88). To make it the more conspicuous in the various illustrations, I have drawn it in unshaded black. This organ is now a mere vestige; it flourished in the remote past. In fig. 60 we have seen that the pineal gland was similar in bird and reptile, the tip of it appearing as a warty projection (P) in front of the largest protuberance of the brain. In the two first heads of fig. 62, it is also discernible. In some recent reptiles, the pineal gland ends in a foramen of the parietal bone, appearing as an odd organ, in the form of an eye, but unable to act as such (fig. 87, 1). In several fossil reptiles and stegocephalians, it served as a third eye.

The little brain or cerebellum (Cb) is large in birds; behind same, the brain runs directly into the medulla oblongata. Though there seems to be no resemblance at all, when we compare the cerebellum in reptile and bird, as

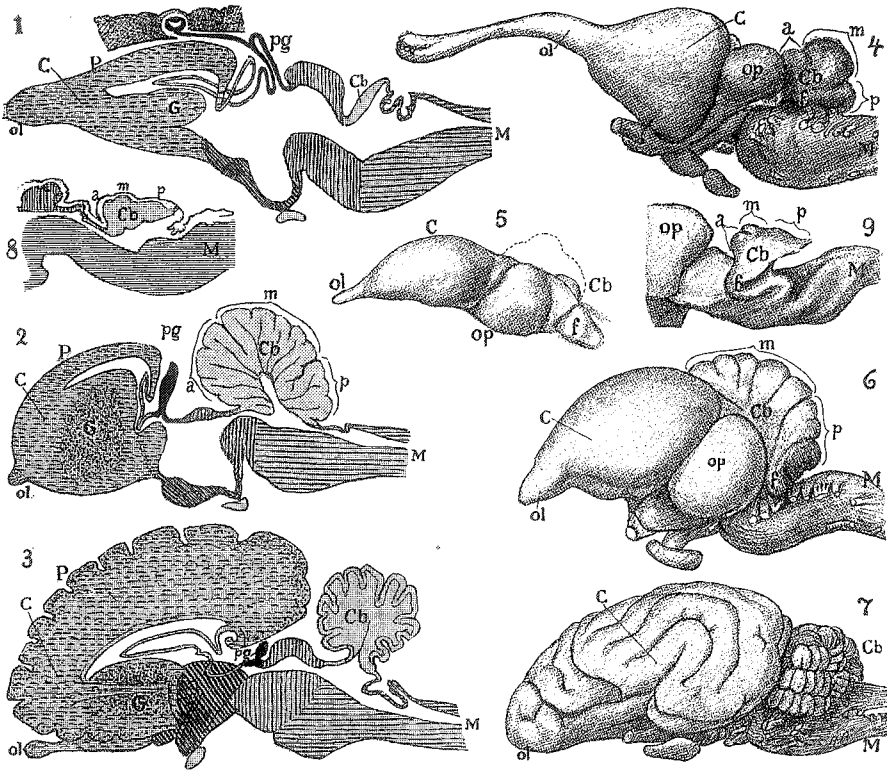


Fig. 87. 1, 2 and 3 schematic longitudinal section through the brains of 1 reptile, 2 bird, and 3 mammal; the corresponding parts of the three brains have the same hatching, after Edinger and Kupffer. In 1 a piece of the brain-case is also seen so as to show the position of the pineal eye. 4, 5, 6, and 7 brains in profile of 4 Alligator, 5 *Scaphognatus Purdoni*, 6 Pigeon, and 7 Pointer, 4 and 7 after Wiederheim, 5 after E. T. Newton. 8 longitudinal section of the hindbrain of a 9½ days chick embryo, 9 hindbrain in profile of same; both after Sven Ingvar. C cerebrum, Cb cerebellum (a anterior, m median and p posterior lobe), f lobus flocculus, G basal ganglia, M medulla oblongata, ol olfactory lobe, cut off in 1, op optic lobe, P pallium, pg pineal gland.

shown in fig. 87, 1 and 2, the bird-embryo passes through a stage in which its cerebellum is but small and strongly reptilian (fig. 87, 8).

In crocodiles, the little brain is better developed and exhibits a distinct transversal furrowing. By two sulcations it is divided into three lobes (fig. 87, 4), anterior (a), median (m), and posterior (p). The last one is characterized by its lateral tapering into two auricles or flock-lobes (*lobi flocculi*, f). In birds, exactly the same tripartition of the cerebellum commences early in embryonic life (fig. 87, 9), but during its further development, each of the three lobes branches into several lobules, as shown in fig. 87, 2, as also in fig. 87, 6 in which the anterior lobe is concealed behind the cerebrum. The

median lobe seems, both ontogenetically (small in fig. 87, 9) and phylogenetically, to be the youngest one (Sven Ingvar, 7).

A complete conformity and homology subsists between each of the three lobes of the cerebellum in crocodiles and birds respectively (7). In both classes, the flock-lobes are protuberances from the posterior lobe; see also fig. 88, 1 and 2. Though the same elements are to be found in the mammalian cerebellum, we see from fig. 88, 3 that this, especially in the median lobe, has

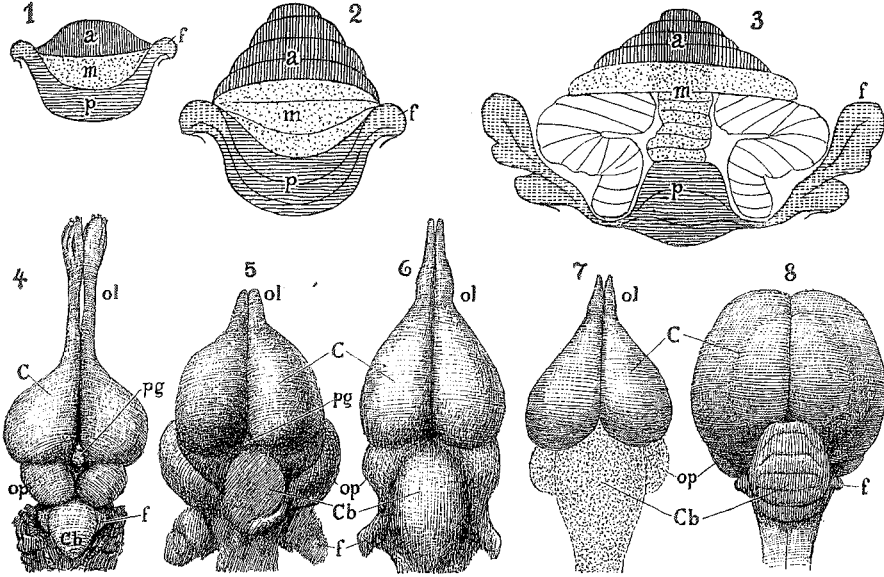


Fig. 88. Schematic view of the cerebellum in 1 Crocodile, 2 bird and 3 mammal, after Sven Ingvar; a, m, p, anterior, median, and posterior lobes. Brains seen from above of 4 Alligator, 5 *Scaphognatus Purdoni* after E. T. Newton, 6 *Hesperornis regalis*, and 7 *Ichthyornis* after Marsh, 8 Pintail (*Dafla acuta*); C cerebrum, Cb cerebellum, f lobus flocculus, ol olfactory lobe, op optic lobe, pg pineal gland.

passed through a different development, while the cerebellum of the bird has preserved just the same line of evolution as that of the reptile (fig. 88, 1 and 2).

The series of brains in fig. 88, 4—8 plainly shows the transitional stages from the reptilian to the bird's brain; in fact, there is a much greater break between the brains of the Cretaceous birds and that of the recent bird, than between the brains of the reptile (fig. 88, 5) and the Cretaceous birds.

Marsh (Odontornithes) says about the brain of *Hesperornis* (fig. 88, 6): "The cerebral hemispheres were of very moderate size, much smaller, proportionally, than in any existing bird, and strongly resembling the corresponding parts in some reptiles". And about the optic lobes: "Their similarity in size and position to the optic lobes of reptiles is especially noteworthy". "The cerebellum was quite large, and reptilian in its general features. The flocculi were well developed, and lodged in distinct cavities".

"The brain of *Ichthyornis* (fig. 88, 7) was remarkably small and, in its main

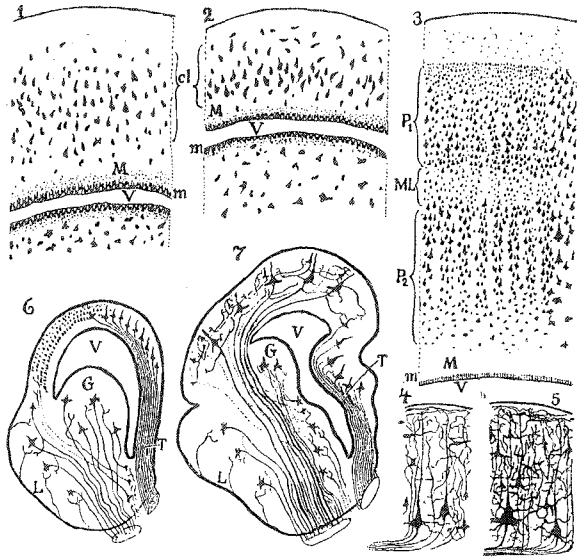
features, strongly reptilian" (Marsh). The olfactory lobes in *Hesperornis* are very large and more reptilian than in the brain of the reptile seen in fig. 88, 5. This brain is of the utmost interest, because it shows to what extent a reptilian brain, in its transformation, may be verging towards that of a bird. It was found as a cast of the brain-cavity, and is described by E. T. Newton (8) as the brain of a Pterosaur, *Scaphognathus Purdoni* (figs. 87, 5 and 88, 5). "Unfortunately, the cerebellum is almost wholly wanting". "It is tolerably clear, however, that the cerebellum extended between the optic lobes, somewhat as in Birds, and that the optic lobes did not separate the cerebrum from the cerebellum, as they do in all Reptiles" (8). In fig. 87, 5, I have indicated, by means of a dotted line, the supposed full extent of the cerebellum. Probably it has been still larger, because the cerebellum is an organ for equilibrium and is well developed in animals moving freely through the medium. A comparison of the brains in fig. 88 will show, more clearly than words can describe, the close affinity between that of the Pterosaur and those of the Cretaceous birds; the cerebrum of the former had also a furrow as in birds. Its flock-lobes (f) were very similar to those in birds. E. T. Newton concludes: "The brain of *Scaphognathus Purdoni* might, indeed, be taken as intermediate between that of Birds and Reptiles, and it certainly makes such a near approach to the brain of *Hesperornis* that one cannot but recognize their close affinity" (8). Another author, H. G. Seeley, says about the brain of Pterosaurs: "I was able to remove the thick covering of cellular bone which originally extended above it, and thus expose evidence that in the mutual relations of the fore and hind parts of the brain, bird and ornithosaur were practically identical. Another Cambridge Greensand skull showed that in the genus *Ornithocheirus* the optic lobes of the brain are developed laterally, as in birds". "The Wealden Pterodactyle *Ornithodesmus* had a similar and bird-like brain" (Dragons of the Air, p. 55).

An examination of the microscopic structure of the cerebrum also goes to prove that the bird's brain is a reptilian brain raised to the highest power of its special development, while the mammalian brain has taken up a new line.

The researches made by Chr. Jacob and Cl. Onelli (9) bring out the fact that the mantle of the cerebral hemispheres (P in fig. 87) does not enter upon a more advanced stage till the reptiles, the proper cortical layer (fig. 89, 1 cl) and the membrane (m) of the cerebral ventricle (V) being completely separated by a new marrow-layer (M). In this cortical layer appear for the first time the pyramidal cells, characteristic of the cerebral cortex of all higher vertebrates.

From fig. 89, 1 and 2 it appears that there is no difference in the build of the mantle of the cerebral hemispheres (pallium) in reptile and bird; it is the basal ganglia which have produced the enlargement of the cerebrum in birds. Chr. Jacob (9) says as follows: "The brain of the bird has not accomplished a higher differentiation, but it shows an enormous increase of the already present old apparatus, which is made more useful by forming commissures and tracts of association; a new principle of build has not appeared, the old style being directly spent".

Fig. 89. Transverse section through the mantle of the cerebral hemisphere of 1 reptile, 2 bird and 3 mammal, somewhat schematic and greatly enlarged; 1 and 2 most, but in the same proportion. 4 schematic diagram of the fiber tracts from and to the pyramidal cells in the pallium of reptile and bird, 5 the same in mammal. 6 and 7 transverse sections through one of the cerebral hemispheres, schematic diagram, to show the fiber tracts in 6 reptile and bird, 7 mammal; all after Chr. Jacob; cl cortical layer with pyramidal cells, G basal ganglia, L olfactory lobe, M marrow-layer, ML middle layer, m membrane of the ventricle, P₁ and P₂ the two layers of pyramidal cells, V ventricle of the cerebrum.



The pallium of mammals, on the other hand, shows a new formation, in contradistinction to that of reptiles and birds, an inserted middle layer (ML) separating the two pyramidal layers (P₁ and P₂). Besides, these layers may divide into several single layers according to the size of the cells.

Another new formation in mammals, no less essential, is suggested in fig. 89, 7. In addition to the fiber tracts T, which in reptiles and birds run in the median wall, there are lateral fiber tracts, extending from the upper and external wall of the pallium, a feature indicating a new plan of build in mammals. As may be seen in fig. 89, 6, lateral fiber tracts are also to be found in birds and reptiles, but these do not originate from the wall of the pallium, but from the basal ganglia G. This shows the conformity of reptiles and birds and their absolute divergence from the mammals.

ORGANS OF SENSE

The organs of sense are the specialized peripheral terminations of the sensory nerves, and they are so constructed as to be capable of receiving only a certain kind of stimulus.

The sense of smell, being of minor importance to reptiles and birds, has not given rise to an external nose, nor is the nasal cavity so close upon the brain as in mammals, the interorbital septum making the distance rather considerable. The same fundamental build and function of the nasal cavity is found in both reptiles and birds; their olfactory lobes have already been compared.

The eye (fig. 90, 1) is Nature's model of a photographic camera. It is a cavity with jet-black walls and an anterior aperture, the pupil, in the coloured iris. Within the pupil lies the lens, which refracts the light-rays in such a

manner as to form an inverted image on the posterior wall of the cavity, where it is perceived by the retina, into which the optic nerve extends. The retina is enclosed by the thin chorioid membrane, and on the outside of this lies the sclera or sclerotic, forming the outer coat of the eyeball. Its anterior portion is the transparent cornea. The interior of the eye consists of the vitreous humor of a gelatinous, colourless consistency.

The ring of ossicles in the sclera of birds has already been mentioned in Part I as an evident inheritance from reptiles. The retina originates from a small part of the cerebrum, constituting an optic nerve and expanding on the inside of the eye (fig. 91, G 2). Its microscopic structure presents peculiarities which seem to show the conformity of the two classes. The light-perceiving organs of the optic nerve fibers end in elongated rods or in more bottle-shaped cones. In reptiles, the rods are comparatively scarce, the cones being predominating, and double-cones frequent. All birds have rods as well as cones, also double-cones being frequent. In both classes, the cones contain drops of fat, mostly red, yellow, and green in colour.

C. Hess (10) has made experiments to ascertain how different animals apprehend the unequal amount of light in the colours. White articles of attractive food were placed on a black substratum and exposed to spectral light, thus assuming the various colours of red, orange, yellow, green, blue, and violet. It now turned out that both reptiles and birds reacted in nearly the same manner, their apprehension of the colours diminishing considerably towards the blue end of the spectrum, a fact fully corresponding with the colours of the drop of fat in the cones of their retina. Altogether, these experiments seem to show a rather close affinity between reptiles and birds in the elements composing the retina.

From the entrance of the optic nerve there is a peculiar wedge-like or rhomboid projection, the pecten (fig. 90, 1 P), running into the vitreous humor. In most birds, it is a single, strongly-pigmented lamella, assuming a variable number of folds. The pecten of the Ostrich has a somewhat different shape, the folds running on both sides from a middle lamella (fig. 90, 2), thus to some extent resembling a truncate cone, and forming a transition to the pecten of the Kiwi, of which G. L. Johnson (11) writes: "Its base is trumpet-shaped, and covers almost the whole of the disc, the margins being moss-like. The process extends nearly as far as the lens in the form of a thick, densely-pigmented brown-black cone without plications".

This remarkable feature strongly reminds us of the corresponding one in reptiles, in which the typical shape of this organ is a cone-like pivot, protruding into the vitreous humor, as if it were an elongation of the optic nerve (fig. 90, 3 and 4). Such a form is found in lizards (fig. 90, 8) and chameleons (fig. 90, 4 and 6); it is not entirely wanting in snakes, but is more pillow-shaped (Virchow 12) in these; in crocodiles, it assumes the veritable shape of a pillow.

Soemmering (13) gives a drawing of the eye of a Monitor, the pecten of which is higher than in most birds (fig. 90, 3). We quote as follows: "From

the entrance of the optic nerve projects a membranous process, nearly cylindrical, enveloped in black pigment, penetrating the vitreous humor, fastened to the lens beneath, reminding one of a stylus, and according to its position and appearance analogous with the pecten of birds". And further: "In the Iguana the process is stronger and broader, forming two plications, approximating more closely the pecten of birds" (13). A strange statement, indeed, more than a century ago, when nobody thought of tracing the origin of birds to the reptiles! The development of the embryo, too, favours the opinion that the pecten in birds and in reptiles are homogeneous formations, because the pecten of the chick-embryo displays no folds until the ninth day, from which

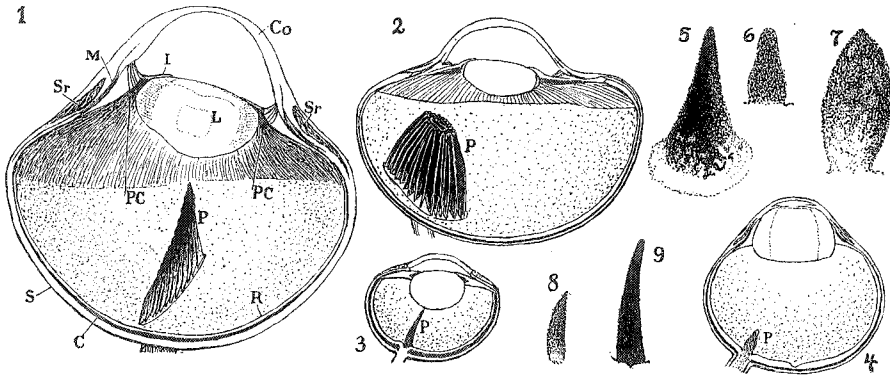


Fig. 90. 1—4 Eyes in longitudinal sections of 1 Sea-eagle (*Haliaeetus albicilla*), 2 young Ostrich, 3 Monitor (*Varanus*), 4 Chameleon, 5—9 pecten of 5 Kiwi, 6 Chameleon, 7 Slow-worm (*Anguis fragilis*), 8 Lizard (*Lacerta viridis*), 9 Monitor. 1 and 2 after V. Franz, 3 and 9 after Soemmering, 4 and 6 after H. Müller, 5 after G. L. Johnson, 7 and 8 after Leydig; C chorioid, Co cornea, I iris, L lens, M ciliary muscle, P pecten, PC ciliary process, R retina, S sclerotic, Sr ossicles in the sclerotic ring.

time they make their gradual appearance. From this fact we may conclude that the pecten of the bird's eye, in all probability, constitutes a further evolution of an organ already present in the eye of reptiles. G. L. Johnson (11) found quite insignificant "vestiges of pecten" in the eye of mammals.

The primary optic vesicles arise as lateral expansions of the anterior end of the neural tube, viewed as a transverse section in fig. 91, G1. G2 gives a transverse section of the same at a later stage, when the lens has already become separated from the ectoderm. The development between these two stages (G1 and G2) is represented in the drawings L2—6 and A1—6, showing how the lens is preformed in reptiles and birds. When the expansion from the neural tube reaches the ectoderm, a thickening of same takes place (A1). The thickening proceeds, expanding and deepening at the same time (L2 and A2), forming an invagination (L3 and A3) in the optic cup. This invagination soon leads to the formation of a deep thick-walled pit (L4 and A4), which rapidly closes (L5 and A5), thus forming an epithelial sac, and the primordium of the lens is complete.

The development of the eye is nearly the same in the various classes; nevertheless, Rabl (14), who has examined the lens of vertebrates very carefully,

says that each class of animals goes its own ways during this development, and that it is impossible to confound the preformation of the lens in mammals with that in birds, reptiles, or other animals. The resemblances in the development of the lens in reptiles and birds, however, are very great, as may be seen from fig. 91; there is, practically, no difference at all. This is further confirmed by the form and position of the cells of this organ.

It is due to its peculiar development that the lens forms an anterior and a

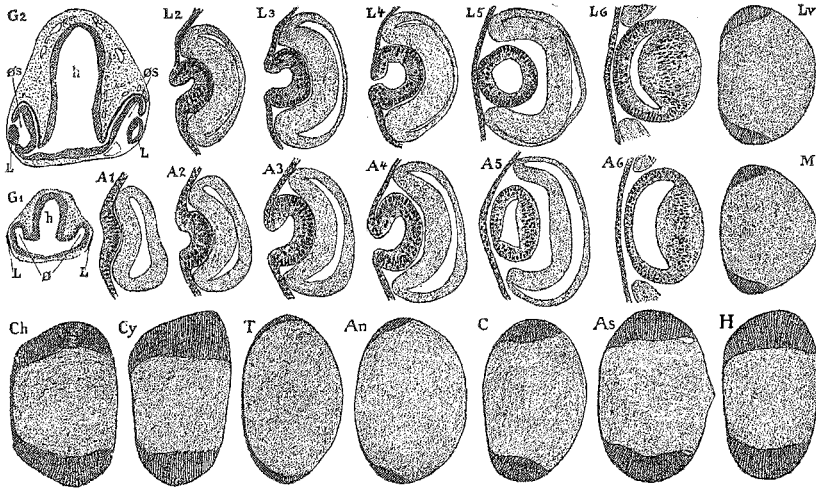


Fig. 91. G 1 transverse section through the forebrain and optic vesicles of a chick-embryo of 16 somites, G 2 the same of an embryo of about 35 somites, both after Lillie; h forebrain, L primordium of the lens, σ optic vesicle, σs optic cup. L 2—6 development of the lens in embryo of Sand-Lizard (*Lacerta agilis*), A 1—6 the same in embryo of Duck (*Anas boscas dom.*); both after C. Rabl. The rest of the illustrations, transverse section of the adult lens in reptiles and birds. An Goose (*Anser dom.*) As Goshawk (*Astur palumbarius*), C Pigeon (*Columba dom.*), Ch Chameleon (*Chamaeleo vulgaris*), Cy Swift (*Cypselus apus*), H Martin (*Hirundo urbana*), Green Lizard (*Lacerta viridis*), M Australian Budgerigar (*Melopsittacus undulatus*), T Common Tortoise (*Testudo græca*); all after C. Rabl. The equatorial ring of the lens in the transverse sections seen as the outer, darker portion.

posterior layer of cells (L 6 and A 6). The posterior one thickens very considerably, constituting the core proper of the lens, while the anterior remains practically unchanged, forming the lens epithelium, which in reptiles and birds produces a peculiar structure, called the equatorial ring, the cells of which change into radially arranged fibers.

In none of the other classes of vertebrates do we find such a ring around the lens, reptiles and birds constituting an exception in this respect. The thickness of the ring varies with each particular species (fig. 91), and is wanting in snakes only.

Rabl (14) supposed that the muscular fibers of the ciliary processes (fig. 90, PC) on the corioid are capable of exercising a pressure on the neighbouring ring, and thus, by means of an increasing bending of the lens, of investing the eye with the power of accommodation. That this really is the case, is fully

confirmed through experiments by Hess (10), who has further shown that the accomodation in mammals is produced in a manner the very reverse of that in reptiles and birds.

The diurnal birds of prey, the small perching birds and especially the swallows, have a very thick ring; in the swifts it is enormous, occupying more than one half of the capacity of the entire lens. Its thickness seems to increase in proportion to the velocity of flight.

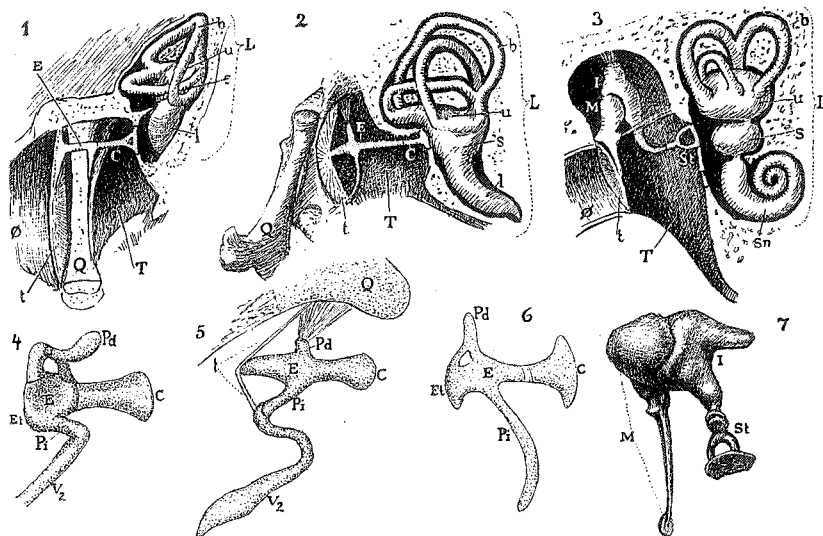


Fig. 92. 1, 2 and 3 schematic illustrations of the inner ear of 1 reptile, after Versluys, 2 bird, partly after Gadow, 3 mammal; 4, 5 and 6 columella, still cartilaginous, in embryos of 4 *Tuatera* (*Sphegnodon*) after Schauinsland, 5 *Hoatzin* (*Opisthocomus*), after W. K. Parker, 6 Kestrel (*Tinnunculus*), after Suschkin; 7 the three auditory ossicles in a horse (*equus*), after Brehm; b semicircular canals, C columella, E extracolumella, Et the part touching the tympanic membrane, I anvil (*incus*), l lagena, L labyrinth, M hammer (*malleus*), Pd upward process and Pi downward process of the extracolumella, Q quadrate, S sacculus, Sn cochlea, St stirrup (*stapes*), t section of the tympanic membrane, T tympanic cavity, u utricle, V₂ second visceral arch, ø external auditory tube.

It is evident that a Swift, flying at a speed of about 300 km an hour, must be able to accomodate remarkably well, much better than a Pigeon, which can cover only 100 km during the same time. This is fully in accordance with the development of the ring in these birds (fig. 91, Cy and C). But what about the Chameleon (Ch), the ring of which has nearly the same size and angular shape as that of the Swift? Not to speak of flying, it hardly ever moves at all, but sticks to the branch onto which it has fastened; and yet, for this very reason, it is bound to strain its power of accomodation to the utmost, and the fact is that it is equipped with this power to an exceptional degree. It is a well-known fact that this droll "prize-shot" caters for himself exclusively by putting out his tongue. Quiet and still as a mouse, he will be on the look-out, keeping the eyes only in constant motion; incessantly they will be scanning the entire surrounding. Swift as lightening, his spear of a

tongue will dart for the fly buzzing past, and his never failing "marksmanship", in hitting his flitting prey, is due to the unique accomodating power of the eye.

Both the ciliary muscle and the sphincter muscle of the iris have striated fibers in reptiles and birds, but not in amphibians and mammals. From this we learn that in its development, build of cells, accommodation, and the surrounding muscles, the lens presents strange and striking harmonies between reptiles and birds.

As a rule, the lower eyelid is the larger as well as the most mobile, both in birds and reptiles; the eyelids of Geckos and Snakes, however, have grown together and are transparent. The nictitating membrane, too, is best developed in the two classes, which by Huxley are joined into one, the Sauropsida.

When we take into account the prominent part played by a bird's eye, being — in its unique acuteness of sight and power of accommodation — more than a match for the eye of most mammals, the more surprising it is that this superior organ, in all essentials, partly is identical with that of the reptile, partly resembles it most strikingly, as a matter of fact, being nothing but a slight evolution of the distinctive features inherent in same. It is the same profound affinity as we found in the build of the brain cortex in reptile and bird. — That the eye of a reptile, also in extrinsic beauty, may equal that of the bird, is seen in fig. 94.

In fig. 92, the inner ear of reptiles and birds may be compared to that of a mammal, and we observe that, while in the first two a single rod only, the columella (C), connects the tympanic membrane with the labyrinth, the mammal has three ossicles: the hammer (*malleus*, M), the anvil (*incus*, I), and the stirrup (*stapes*, S). An examination of the visceral arches of embryos will show us that these three ossicles have the same preformation, respectively, as the articular, the quadrate, and the bony parts of the columella, in reptiles and birds. The mammals have no quadrate, and their mandible consists mainly of the dentary, while the angular of the reptile has become the bony ring (*tympanicum*), across which the tympanic membrane is suspended. This leaves a considerable gap between reptiles and birds on the one hand, and mammals on the other.

The proximal part of the columella is bony, the distal one cartilaginous, and is called extracolumella (E). This sends out three processes. That these, as well as the entire columella, are nearly identical in reptiles and birds, is seen from fig. 92, 4, 5, and 6. The lagena (fig. 92, 1 and 2, l) corresponds to the cochlea (Sn) of mammals; in the former, the acoustic organs are supported by distended strings of equal length; in the cochlea, they are of different lengths.

SEXUAL ORGANS

The digestive organs are, as might be expected, in all essentials, the same in the two classes. Gadow (29) remarks that the cæca of birds are an inheritance from reptiles.

The sexual organs of birds and reptiles debouch into the cloaca, and

especially the male organ (*penis*) seems to present peculiar features, shared by both classes.

We find the development of this organ most grotesque in lizards and snakes, the penis of which is bifold. Under the skin of the tail-root, just behind the transverse anus, there are two hollow cul-de-sacs, one on each sides, at the corners of the anus; these may be turned inside out, being reversible like the finger of a glove. Each has a deep spiral furrow, and, in some species, the point is bifurcated. During the act of copulation only one of these organs at a time is in function, after which, retracted by a muscle, it reverts to its original position.

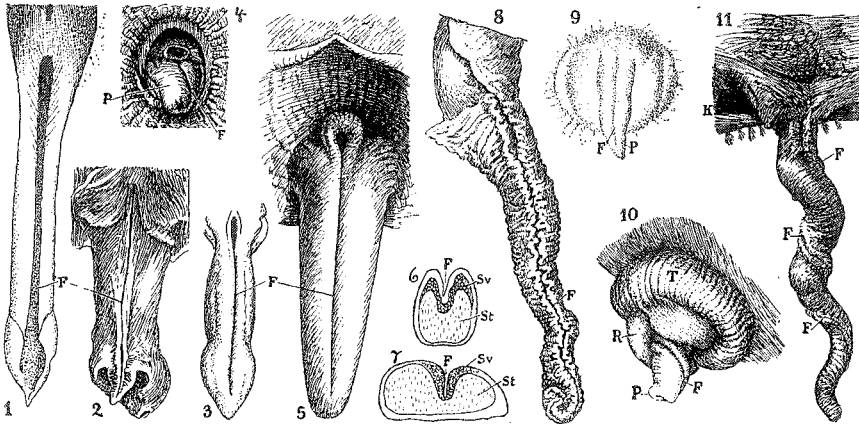


Fig. 93. The male copulatory organ, penis, in reptiles and birds; 1 Common Tortoise (*Testudo graeca*) after Gadow, 2 Crocodile after U. Gerhardt, 3 Mud-Tortoise (*Emys*), after R. Wagener and Bojanus, 4 Cassowary, the external opening of the cloaca, penis not reversed, and 5 Ostrich, both after Geoffroy St. Hilaire, 6 Turtle (*Thalassochelys corticata*), transverse section after U. Gerhardt, 7 Ostrich, transverse section after Boas, 8 Rhea, the blind sac reversed, after J. Müller, 9 Tinamou (*Crypturus*) after J. Müller, 10 embryo of Duck on the 22. day, enlarged after C. Pomayer, 11 Mallard (*Anas boschas*), reversed (nat. size), behind is seen a part of the wall of the cloaca (K); F furrow through which the semen is directed, P penis, R secondary ring-wall, St supporting tissue, Sv spongy tissue, T fluted ring-wall of the anus.

In tortoises and crocodiles, the organ consists of a single, lengthwise symmetrical, protuberance, in the middle of the ventral wall of the vestibulum of the cloaca, and in the median line of the free part there is a longitudinal furrow for the transmission of the semen (fig. 93, 1, 2, 3). The penis is not a hollow, but a compact organ, the free end of which, when erected, may protrude considerably beyond the anus, for the longitudinal furrow is interwoven with swampy tissue, which expands and becomes erect when filled with blood, and is supported by fibrous connective tissue (see fig. 93, 6).

A penis quite similar to this, is found in the Ostrich (*Struthio camelus*). This is also a single and compact organ, attached to the ventral wall of the vestibulum of the cloaca, and with a longitudinal furrow on its dorsal side (fig. 93, 5). It contains both spongy and connective tissues (fig. 93, 7), as also an elastic portion. The penis of the Kiwi (*Apteryx*), too, is quite similar.

An entirely different kind of penis do we find in the other Struthious Birds: Rhea, Cassowary, and Emeu, as also in the duck tribe: Ducks, Geese, and Swans. It is a rather curious fact that the build of this organ reminds one considerably of that of lizards and snakes, but it is not bifold. It consists of a small, very fibrous, projection from the ventral wall of the vestibulum of the cloaca, and on the top of it there is an opening, leading to a revertible cul-de-sac. The appearance of same in Rhea, when everted, is shown in fig. 93, 8; we see a spirally twisted furrow, bounded by projecting edges, running along its surface. Homologous to this is the penis of Cassowary and Emeu. In the Mallard it is well developed, and of a somewhat vermiform appearance; its spiral turn is very conspicuous (fig. 93, 11). The size of penis, however, varies considerably in the different species of ducks. In all other birds the penis is entirely wanting, and the primitive way of everting the cloaca during copulation is resorted to. The furrow for the transmission of the semen has, in the case of mammals, become a closed channel, at the same time doing service as a urethra.

The obvious and striking similarity between the penes of the Ostrich, the crocodiles, and the tortoises require no further demonstration. That of the Kiwi is of a similar kind. Says U. Gerhardt (15): "Penis in *Apteryx* exhibits the same component parts as that of the reptiles in question: the only difference consists in the strong asymmetry in the bird".

The penis of the Ostrich is homologous in development to those of crocodiles and tortoises. The preformation in all of these makes its first appearance at the orale edge or lip of the anus. This, however, holds good of the other birds as well. C. Pomayer (16), who has made Duck-embryos a special study, says that the penis "originates in birds, as in reptiles, from the orale lip of the anus and is surely a part of same, specially adapted to this end". About the 8th day, this part assumes a pointed and conical shape, the preformation of a penis. Not until later does the cul-de-sac originate from this point; still later (11—13th day) does a spiral twisting of the projection take place, and the inverting process begins. At this time, too, a secondary protuberating ring, shaped like a horseshoe, appears, enclosing the preformation of the penis (fig. 93, 10 R), but the fluted ring-wall (T) soon develops so as to cover the penis-preformation, which, exteriorly, disappears to view. According to Pomayer (16), the development of the penis in the Ostrich-embryo runs parallel with that of the Duck-embryo, but without the formation of a cul-de-sac.

The preformation of the copulatory organ in lizards and snakes, strangely enough, also commences from the orale lip of the anus, but as two compact processes from the lateral parts of same. They originate; consequently, as in the other reptiles and in birds, from the ventral wall of the vestibulum of the cloaca, developing outwardly; not until later are they transformed into inverted sacs (Unterhössel, 16). According to Hellmuth (16) does the penis of tortoises undergo "the same process of formation as lizards and snakes", and, in the Pond Tortoise (*Emys*) he found the preformation commencing as two processes. Rathke (16) relates the same thing about the Soft Tortoise (*Trionyx*).

In several genera of this family (*Trionychidæ*) does the penis, when developed, end in a spout-shaped projection on either side of the point (C. K. Hoffmann, 17), thus bearing the unmistakable impress of its bifold origin.

The results arrived at bear evidence of the very striking resemblance, both as to development, structure, and build, of the copulatory organ in reptiles and birds.

As intimated above, the bird's penis is an organ about to disappear, and in most birds it has already done so entirely. In the embryo of the Carrion Crow (*Corvus corone*), the Jackdaw (*Corvus monedula*), and the Common Coot (*Fulica atra*), Pomayer (16) has called attention to a penis-formation corresponding to that of the Duck-embryo. But the organ is entirely wanting in the adult birds. Thus once more we witness the embryonic development bearing upon the past.

SECONDARY SEXUAL CHARACTERS

The peculiarities which, apart from the sexual glands, distinguish the male and female respectively, are called secondary sexual characters. The forms under which these manifest themselves are multifarious, peculiar, and conspicuous, as far as the reptiles are concerned, in this respect second only to the birds. Amongst the reptiles we meet, as it were, the forerunners of this profusion of sexual characters in birds. In both, the colours are, so to speak, applied more unmixed from Nature's palette and, in the case of the birds particularly, fondness of display is more pronounced than in the mammals. I take it for granted that the secondary sexual characters in birds are universally known, and shall therefore chiefly deal with some of those pertaining to the reptiles. Exteriorly, the sexual differences are distinguished by outgrowths of skin and horn (throat-pouch, crests, spurs, and horns); dimensions (size of head, length of tail, total length); divergence in colour and markings; and in number of scale series.

Horns are found on the males of several Agama Lizards; the Horned Lizard (*Ceratophora*), for instance, has one on the tip of the nozzle; in other species, the horn-processes of the head may change into a dorsal crest. But especially in Chameleons from Africa and Madagascar do we find a rich development of horns in front of the eyes. Thus the male of Johnston's Chameleon has three peculiar horns, and the Long-nosed Chameleon (*Ch. xenorhinus*), an immense projection on the nose, and also one across the top of the skull.

The heads of Chameleons, moreover, may be adorned with rounded or elongated and pointed flaps of skin, an ornament also worn by the Basilisks, the males of all four species of which have a tall process on the back part of the head; *Basiliscus plumifrons* has even two such excrescences, one on the forehead and one on the scruff of the neck, and, moreover, an immense dorsal crest. The males of several Iguanas, too, wear similar excrescences, e. g. Rhinoceros Iguana (*Metopocerus cornutus*), the proud head of which, with its beautiful and vivacious eyes, is illustrated in fig. 94. Like the other Iguanas

and a great many other Lizards, it has an inflatable throat-pouch, expanding when stirred by emotions of anger or love on the part of the animal. I merely wish to call attention to the Gallinaceous birds, the males of which also possess skin-flaps, besides several variegated warty excrescences, more or less inflatable and erectile. Thus, when inflated, the air-bag at the side of the neck of the cock Prairie-hen (*Tympanuchus americanus*), is like a small orange; the Mexican Crested Curassow (*Crax globiera*) is furnished, at the root of the beak, with a big, yellow, rounded projection. Lord Derby's Guan (*Oreophasis derbianus*) wears, on the forehead, just between the eyes, an

upright horn of a deep scarlet colour; and the Crimson Tragopan (*Tragopan satyra*) has, behind either eye, a small, conical, fleshy horn bending forwards, erectile during the mating season. The peculiar, erectile, dermal processes, at the root of the beak, of the males of several Bell-Birds, belong to the same category. Horn-formations on the upper beak, are met with in several Hornbills (*Bucorax*, *Ceratogynna*, *Dichoceros*, *Rhytidoceros*, *Bycanistes*, *Rhinoplax*), in both sexes, it is true, but

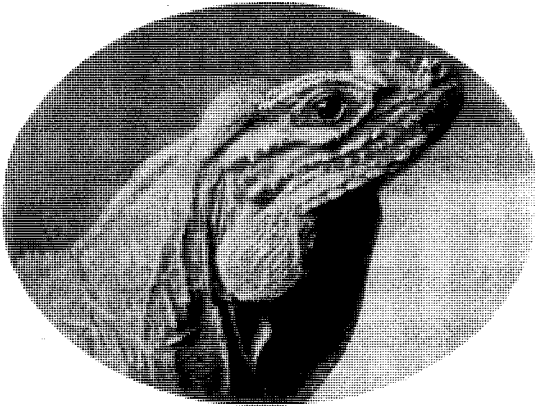


Fig. 94. Head of male Rhinoceros Iguana (*Metapocerus cornutus*); photo by Medland.

less pronounced in the female. Sir Harry Johnston says about *Ceratogynna elata* ("Liberia", Vol. II p. 782): "In the females and in young males there is very little variation in the rounded outline of the ridge, but in adult males this swells at the sides and develops into a permanent "horn". The Hornsbills, too, have richly coloured, bare dermal ornaments.

Just as in the case of birds, the male of reptiles, as a rule, is larger than the female, but in both classes there are exceptions (most birds of prey, some Waders, viviparous Lizards, the Slow-worm, some species of Soft Tortoises, Water-snakes).

The differences in colour and markings for the two sexes may also be very conspicuous in both classes, and the brilliancy of colours increases during the breeding season. I shall confine myself to mentioning the divergences of the male from the female in some species. Tuatera (*Sphenodon*) has a black shoulder spot, a fine violet-coloured throat with white longitudinal stripes. According to Reese (18), a richer colouring of the *Alligator mississippiensis* sets in during the breeding season: spots, stripes, and a lighter yellow instead of a dirty green, red spots under the eye. The Wall-lizard (*Lacerta muralis*) has a red belly, a dotted back, and azure sides; the female, a white belly and an unspotted back. So also *L. fiumana* and *L. peloponnesica*, a yellowish-

red belly, the former, a blue shoulder spot as well. In the Green Lizard (*L. viridis*), the throat is blue or rose-coloured, while the female frequently has longitudinal stripes, and a white, light blue, or pink throat. The Algerian Keeled Lizard (*Psammodromus algirus*) displays one or two golden, longitudinal stripes, within black borders, on the sides of the body, and a bright, blue eye-spot, enclosed in a black wreath, at the shoulder. The Black-spotted Keel Lizard (*Algiroides nigropunctatus*) has a magnificent blue throat and a flame-coloured belly. In males of the Changeable Lizard (*Calotes*), the change of colours is great, compared to that of the females. The same thing holds true of *Liolepis belli*; more-

over, the male is capable of flattening his body, so as to make an exhibition of the colours. In the pugnacious males of several Anolis Iguanas, the intensely red throat-pouch becomes inflated during the breeding season. The throat-pouch of the Malay Flying Lizard (*Draco volans*) is citrinous, the colour blazing up by glimpses; that of the female is slightly bluish. Flower (19) says about the male that, when flying, it looks like a flashing gem. In the Rough-tailed Aga-

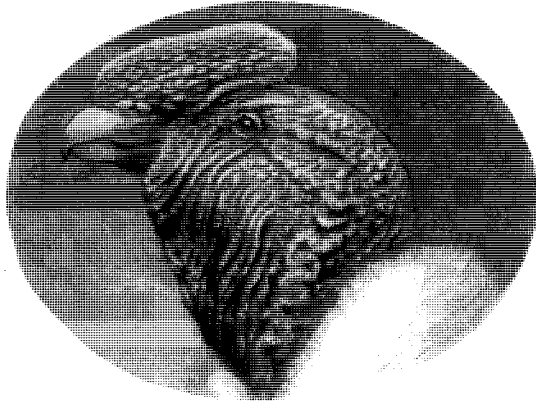


Fig. 95. Head of male Condor (*Sarcoramphus gryphus*) from a photograph.

ma (*Agama stellio*), the sexual instinct gives rise to brick-coloured parts at the scruff of the neck, and on the top of the head. Rather magnificent is the Spiny Agama (*Agama colonorum*), the head of which is flame-red, the body and limbs deep steel-blue, while along the middle of the back generally runs a whitish line; the tail is red and blue. The female is plain brown, with a lighter shade along the back, and the young males are like her. The same thing holds true of other Agamas; the throat-pouch may be a beautiful blue, yellow, or red, or else adorned with blue longitudinal stripes. In a kind of Skink (*Mabuia quinquetæniata*), too, the sexes are very different; the female has preserved the longitudinal streakings of the young. — In this connection it suffices to point out the difference in colour between the male and female of the Bird of Paradise, several species of Widow-finches and Honey-suckers, Humming-birds, Gallinaceous birds, and the Ostrich.

The mammals have no real love-displays; at any rate, nothing at all recalling those practised by the birds; but in reptiles we meet with primary indications of same. Male reptiles are nearly always on the war-path. The Wall-Gecko (*Tarentola annularis*) is reputed for its nocturnal combats, accompanied by quacking, serious wounds, and paralysed jaws. The Iguanas are very irascible during the mating season; his throat-pouch swelling, the male will

rush at his opponent; both of them will try to seize each other with their teeth, at the same time lashing out with their powerful tails. Nicolson (19), in speaking of the Anolis, states that as soon as a male catches sight of another, he runs quickly up to him, who as a brave hero, prepares to fight. Before closing in, they turn about each other like cocks, moving their heads vehemently and rapidly up and down, inflating their throats, and darting fiery glances at each other. The attack follows, and when both opponents are equally strong, the scuffle will keep on for a long time. It generally ends in the loss of a tail, which is devoured by the victor. The females approach as if enjoying, but without joining, the mêlée. Tofohr (19), in speaking of the Eyed Lizard (*Lacerta ocellata*), says that the males will dart for each other and close in deadly combat, biting each other's head, belly, legs, or jaws, and whirling round each other at a furious rate. W. A. Lamborn (20) has observed that two males of the Spiny Agama (*Agama colonorum*), when fighting, will place their bodies parallel, and in such a way that the head of one faces the tail of the other, and vice versa. Either endeavours to gain the best position, for the point is to overpower the opponent by a few well directed strokes of the tail. The animals are very adroit in jumping aside to evade each other's strokes, sounding as loud smacks. Crocodiles and tortoises fight, too, the former bursting out in a kind of barks during the contest.

It must be considered a love-display, on the other hand, when the male of the Alligator, inflated, floats about in the water, raising his head and tail, and turning around in front of the female. The love-displays of the various lizards, are much alike. Hesse (21), in speaking of the Wall-lizard (*L. muralis*), and Leydig (22), of the Sand-lizard (*L. agilis*), relate how the male, his back peculiarly curved and uneven, trunk compressed, and tail standing upright in a curve, will approach the female, and gently lay hold of her scruff. The female responds by some quivering motions of her hind-part and tail, "opens the mouth towards the male, as if going to say something to him, which evidently sticks in her throat". According to Tofohr (19) does the male of the Eyed Lizard (*L. ocellata*) approach the female, his head bending low, his back rounded like a tom-cat's, his whole body strangely compressed, so that it looks considerably taller and more arched. His legs straight as candles, the amorous male struts about the object of his affection. This is said to be a very droll spectacle indeed. Bauhof (19) says about tortoises that the male will incessantly make love, run about uneasily, sniff at the female, and try to rouse her attention by snaps and raps.

All this, of course, is not very much, compared to what the male bird is capable of producing by way of colours, songs, and dances. Yet, when the Changeable Lizard (*Calotes emma*), with raised fore-part and swelling throat-pouch, the latter showing a dark spot, boldly defined against a yellowish-red, approaches the female (Doflein, 21), it is the same desire to display his beauty, which makes the peacock unfold his gorgeous tail. Song, in its proper sense, the reptiles are unable to produce, but it must be borne in mind that the real singing-birds comprise only a few, highly developed species. The power of

producing other sounds, however, is conspicuous during the breeding season. When, for instance, the male crocodile will bellow (like a calf or a bull, says Hagmann, 23) to attract the attention of the female, we may compare it to the pairing-cry of the Bittern (*Botaurus stellaris*), and of the Rhea, which also constitutes a kind of bellowing. The Stork cackles with its beak; by hammering on a dry branch, the Woodpecker sets it vibrating so as to produce a buzzing note. The Jack-snipe (*Gallinago scolopacina*), during the breeding season, while exhibiting its art of flying, produces a strange, bleating sound, caused by the vibration of the two stiff and peculiarly shaped outer tail-feathers. A Pennsylvanian Mud-terrapin (*Cinosternum*) wears on his hind legs two rows of horny warts, which, on rubbing against each other, produce a note similar in sound to that of the grasshoppers. The Geckos (*Teratoscincus* and *Ptenopus*), too, may produce similar notes by means of the peculiar caudal scale-rings, which, however, are common to both sexes.

Amongst the birds it is obvious that the contests carried on, originally in dead earnest, between the males of the various species, have gradually been superceded by mere sham fights, and the transition from these to dances, is natural enough. In the jungles of Ceylon, Doflein (21) has been watching the fights carried on between Wild Cocks (*Gallus stanleyi*), and their scuffles were often so violent that one of the antagonists was left dead on the battle-field. Our Ruffs (*Machetes pugnax*), on the other hand, wage their battles partly as a fight, and partly as a dance. The same thing may be observed by any one watching the erotic frolics of our Sparrows (*Passer dom.*) in spring. Schomburgk (21) describes the dance of the gorgeous orange-coloured Cock of the Rock (*Rupicola aurantia*) as something exceedingly graceful, the males appearing, one by one, on a flat rock, surrounded by numerous spectators, amongst which the females, plainly clad in a homely brown, loudly applaud the performance of each. Other birds have gone a step further, both sexes taking part in the ball. The dance of the Cranes (*Gruidæ*) is of such repute as to be practically proverbial. At the matching-dances of the South American Ypacaha (*Aramides ypacaha*), and of the Jacana (*Jacana jacana*), both sexes join in the frolics.

Amongst the reptiles, no dancing has as yet been observed; but as their love-displays have only casually and desultarily been watched, it is impossible to form any adequate idea of what really does take place in this respect. According to Hilzheimer (24), the love-sports of Turtles recall those of birds. This statement is rather surprising on first thought; but when we learn from Brehm (19) that their stupendous dexterity and skill in water is comparable with the corresponding accomplishments displayed by birds of prey in the air, the fact at once becomes intelligible. As a matter of fact, birds of prey, particularly, achieve their splendid feats on the wing during the breeding season.

The secondary sexual characters in reptiles and birds may be compared to the rhythm of symphony — probably due the fact that their brains are homologous in build and structure —, while those of the mammals are in an altogether different key.

Most birds live in pairs; some of the Gallinaceous birds, however, are polygamous, while, for instance, the genuine Cuckoos (*Cuculidæ*) match promiscuously. In the reptiles, the last practice is most commonly observed, but close investigations, particularly in this field, have not been made. W. A. Lamborn (20) has pointed out that the Spiny Agama (*Agama colonorum*) joins in a small community, comprising 6—7 females and one male. They regard him as their liege lord, gather day by day in the same place, and both sexes roost together. The male maintains strict discipline, and the females stand in awe of him. This is obviously a mode of cohabitation very much similar to that of the Gallinaceous birds. That a couple of reptiles should keep together for any length of time, is evidently a matter of very rare occurrence. The Gopher Tortoise (*Testudo polyphemus*), nevertheless, is said to live, mated two and two, in self-constructed caves. So does the *Liolepis belli*, and Annandale says that the pair hold together faithfully. According to Werner (25) does the Eyed Lizard (*Lacerta ocellata*) in Algiers (*var. pater*) live in pairs after the breeding season; and so do the Green Lizard (*L. viridis*), the Ring-tailed Iguanas (*Cyclura carinata*), the Wall-lizard (*L. muralis*), and the Indian Cobra (21).

Hatching of eggs by means of increased caloricity, may be met with in reptiles. F. Doflein (21) had occasion, in Colombo, to study the specimen of an Indian Python, reproduced in fig. 96. For 11 weeks on end, the mother, coiled up, lay on her eggs, more than one hundred in number, without taking any nourishment whatever. After the young had left the eggs, Doflein witnessed, to his amazement, that every evening they returned to their shells, round which the mother remained in the same position. The temperature of a hatching Python rises to 10—12° C. above that of the surroundings. Alligators and Caimans will construct a nest from bits of plants, taking care to choose a damp site, lay the eggs, and cover them up. Owing to the moisture of the subsoil, the vegetable substance will ferment and decay, thus raising the temperature sufficiently to hatch the eggs. All eye-witnesses agree that such a nest will reek when uncovered. The eggs of the Nile Crocodile, on the contrary, are interred in dry sand and hatched by means of solar warmth.

Strange to say, the same mode of incubation subsists for birds as well. The Megapodes (*Megapodiidæ*) have altogether abandoned the mode of direct hatching. According to Wallace (26), the Maleo (*Megacephalum maleo*) in Celebes will dig a hole in the sandy beach, gradually deposit her eggs in same, and cover them up. The bird bestows no more care on them, but leaves the warmth of the sun to do the rest. The young will emerge of their own accord, and at once run into the forest. Sarasin (21) has seen them, to this end, even resort to sand near thermal waters or volcanos. Corresponding reports on other species (*Megapodius wallacei* and *M. brenchleyi*) from other islands, are not wanting. A somewhat different stage of the same mode of incubation, is represented by the South Australian Mali-fowl (*Lipoa ocellata*), which knows how to regulate the temperature of her self-made incubator, a mound of sand mixed with fermenting vegetable substance. Guided by the weather, she combines the heat arising from the fermenting weeds with the

solar warmth. A third mode of incubation is peculiar to the Megapodes in North Australia and New Guinea. Of various weeds they build up a high mound in the dense underwood, safe from the rays of the sun, thus availing themselves exclusively of the heat generated by the fermenting process, for hatching their eggs, exactly like the Caiman and the Alligator. The mode of incubation in the Maleo, corresponds to that of the Nile Crocodile. "These mounds are also used by reptiles, for out of one I dug, besides the megapode's eggs, about a dozen eggs of some large lizard" (Davison, 26). The resemblance to reptiles, in their modes of incubation, can hardly be carried further.

One of Nature's freaks seems to have been the contriving of little pitfalls for rash scientists. As a matter of fact, several of these — nomina sunt odiosa — have tumbled in, hand over fist, when trying to make out that the mode of incubation practised by the Megapodes, constitutes a direct inheritance from the reptiles. It is easy to prove the fallacy of this statement. As pointed out above, Pycraft (6) has called attention to the fact that the *Megapodiidae* bear evidence of the same break in the development of their distal primaries, as took place in the young of the other Gallinaceous birds (fig. 85). This is conclusive evidence that these birds, too, at an earlier period, built their nests in trees, and that their young climbed the branches. The present mode of incubation, therefore, is a secondary adaptation, an atavism, so to speak, but no direct continuation of an original condition.

The nursing of nestlings, similar to what takes place in birds, we cannot, of course, expect in reptiles. Only a few species manifest a slight tendency in this direction. The female Caiman will constantly guard the mound containing her nest, nourish her young, and fearlessly defend them at the risk of her own life (Schomburgk, 19). The Nile Crocodile will sleep at night at the place where the eggs are buried; and in Madagascar, Voeltzkow (27) made the interesting discovery that the young crocodiles in their eggs, just before hatching, would give vent to sounds on any shaking of the ground in which their eggs were deposited. Lamborn (20) characterized these sounds as croaking. Hence, the mother is able to hear when the time is due for digging them out, and the young ones cry out, evidently because they have an undefined conception that something is wrong, with which they are unable to cope, for they cannot extricate themselves, and will die if left where they are. Strange to say, something similar has been observed in the young of birds. When

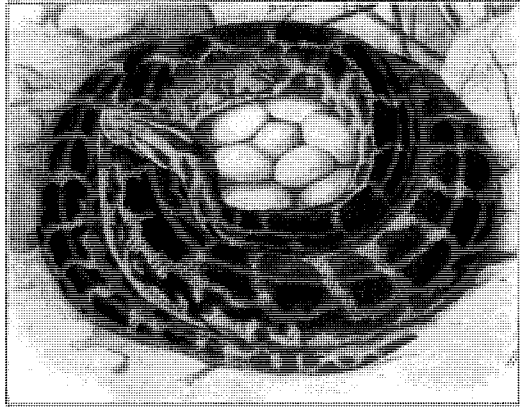


Fig. 96. Indian Python (*Python molurus*), brooding its eggs; after F. Doflein.

in 1917 A. L. V. Manniche (25), in the north-east parts of Greenland, according to his own account, looked up a nest of White Gerfalcon (*Falco gyrfalco*), in order to secure the young, supposed to have been lately hatched, the eggs were still unbroken. So he took these with him, but on their cooling down very considerably, he plainly heard the hoarse shrieking from within the eggs. By placing them on his body under his clothes, he succeeded in making up for the mother, until the first young one was hatched on the following day.

OTHER ORGANS

In Part II we have pointed out the homologous development of most of the inner organs in reptiles and birds. In both classes, moreover, the red blood-corpuscles are oval in shape, while circular in mammals (oval in the camel and the llama, however). The mammals have a complete partition-wall between the two cavities containing the heart and lungs, and the abdomen, respectively. It is called the diaphragm, and constitutes an important respiratory muscle. In Sauropsida we find nothing corresponding to this. The crocodiles are an exception in this respect, corresponding to neither mammals nor birds. In birds the organ consists of two parts, with air-bags between, but differs from that of mammals in position, function, and structure.

As generally known, the air passes into the lungs through the windpipe (*trachea*), which bifurcates into two *bronchi*, leading to the two lungs. The upper part of the windpipe consists of the larynx, a ring-shaped cartilaginous frame, supporting two folds of mucous membrane, the so-called vocal cords. In passing through these, when they are tense and close together, the air is set vibrating, thus producing sound. Unlike mammals and reptiles, however, the birds produce no sound by means of the regular larynx; for song and intonation they possess a secondary organ (*syrinx*), situated at the place where the windpipe bifurcates into the two bronchi. It must no doubt be regarded as a recently acquired organ, and is present in both sexes, but in the special singing-birds the syrinx of the male is much more complex in structure than that of the female.

From the bifurcations of the windpipe in several Penguins (*Spheniscidæ*) and Petrels (*Tubinares*), a partition-wall may extend into a part of the windpipe. Such a partition of the respiratory duct, may also be found in a number of tortoises. According to several authors (Wunderlich, Watson, Fürbringer, 29), this partition-wall still represents what is present in the embryo, the two lung-bronchi of which have not as yet fused into one undivided tube (fig. 97), — thus furnishing a hint as to what the two classes once may have had in common.

As a matter of fact, the lungs of the embryo commence as two small, everted parts of the fore-gut (which latter is subsequently transformed into gullet and stomach). These two parts grow into elongated sacs, the upper extremities of which are the upper bronchi, while the lower ones constitute the branches of the bronchial tubes. From either of these, several small

vesicles grow out, into the lung sac, until gradually the minute ramifications of the lungs have been developed. The whole arrangement will be best understood by a reference to fig. 97, a—e (Selenka 30).

The phylogenetic evolution of the lung has no doubt taken the same course. The different stages of development are still traceable through the classes of vertebrates. In some amphibians, the lungs are as yet nothing but two, nearly tubular, sacs, the inside of which is entirely smooth; in others, the sacs bulge out, more or less, thus of course increasing the aërating surface. A similar

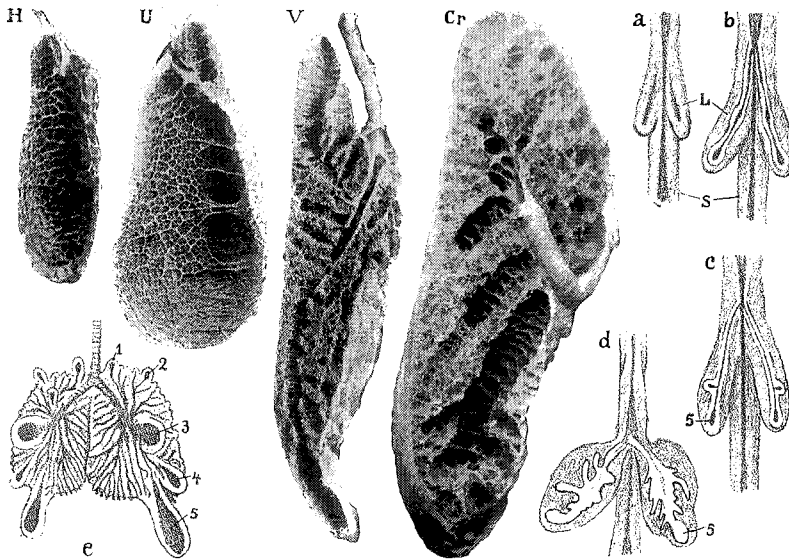


Fig. 97. Longitudinal section of lungs of reptiles: H Tuatera (*Sphenodon*), U Spiny-tailed Lizard (*Uromastix*), V Monitor (*Varanus bengalensis*) photographs after Hesse; Cr Crocodile after photograph by H. G. Herring; a, b, c, d and e show the development of the lungs of a chick-embryo; L primordium of lung; S œsophagus, 1—5 preformations of air-sacs, after Selenka.

arrangement is met with in Tuatera (*Sphenodon*), the lungs of which consist of sacs with a great number of bulging, vesicular parts of the wall (fig. 97, H). The parts of the wall resisting this expansion, are seen as lists, projecting into the cavity of the lung. In higher classes of reptiles, the cavity grows more and more complex (U and V), gradually disappearing as such, by a transformation assuming a more spongy consistency (Cr). F. Moser (31), who has studied the lung-development in embryos of the various vertebrates, writes as follows: "There can hardly be any doubt that the lungs of the higher reptiles constitute a direct transition to those of birds on the one hand, and of mammals on the other". And further: "The lung of the reptiles develops exactly like that of the bird-embryo".

Still more striking is the fact that the air-sacs communicating with the respiratory organs of the birds, and apparently a special feature of theirs, also have their prototype in the reptilian lung. "Just as in birds is the extremity

of either bronchus [of the reptiles] capable of expanding considerably, and grow into an air-sac" (F. Moser, 31). In the lung of the Varan (fig. 97, V), we see how the branches of the bronchial tubes, at their upper and lower extremities, end in such dilatations, and a comparison with the lung of the Hen-embryo (e), will throw light on the same fact. The preformation of the air-sacs of the latter, appears as vesicles at the end of the branches of the bronchial tubes. The excellent photo of a Chameleon-lung (fig. 98) plainly shows what a reptilian lung may attain to, in the way of air-sacs.

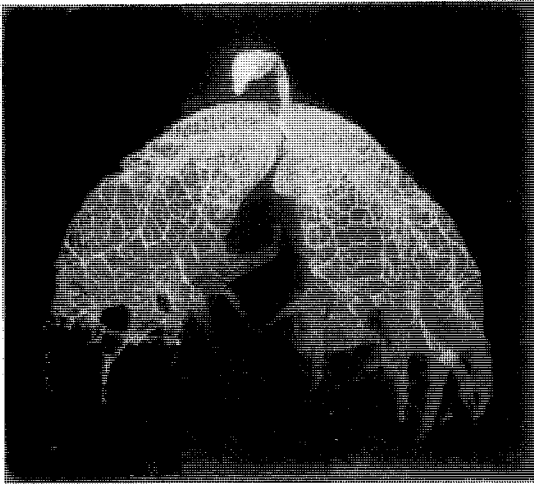


Fig. 98. Lung of Chameleon with the air-sacs; photograph by H. G. Herring.

It would take up too much room by far, were we to enter into details about the various muscles of reptiles and birds. No small part of them, moreover, is found in mammals, transformed, of course, according to the variegated use of the limbs. So we must confine ourselves to one muscle, which is peculiar to reptiles and birds, it being present in neither amphibians nor mammals. It is called the ambiens muscle (*musculus ambiens*), in reptiles (fig. 99, 1) originating from the ilium, at the point where the latter joins the pubis; from here the muscle runs along the inner surface of the thigh, ending in a long, slender tendon, which passes obliquely across the knee-joint; then, between the different tendons of *m. femoro-tibialis*, and below these join the tendon of *m. peroneus posterior* (fig. 99, 3). An exactly similar muscle is present in birds. It may, in the Ostrich, originate from the same part of the ilium as in reptiles, but as a rule it originates from the pectineal process, which also is a part of the ilium (see fig. 10); or it may, in a few cases, as e. g. in the Loon and in some ducks, originate from the anterior part of the pubis. Otherwise, the position of the muscle is exactly the same as in reptiles, its long tendon passing obliquely across the knee-joint, and joining the tendon of *m. flexor perforatus* (fig. 99, 4, 5, 6), which, according to Gadow (29) is partly traceable to *m. peroneus posterior* of the reptiles. A further indication that the ambiens muscle is an inheritance from the reptiles, is that in most birds it is fast dwindling, while in some it has already disappeared altogether.

The skin of reptiles and birds, in contradistinction to that of amphibians and mammals, is but sparingly provided with dermal glands; thus, for instance, they do not sweat. The horny sheath of the epidermis of the reptiles is renewed either wholly or in parts; and somewhat the same thing holds

true of a few birds; a Puffin (*Fratercula arctica*) sheds the epidermis of its beak every year. Bartlett (35) has observed that Penguins, when moulting, cast off their short scale-like feathers from their wings in a manner that he compares to "the shedding of the skin of a serpent".

The horny sheath of the beak of several birds, is composed of more parts than one, and E. Lönnberg (32) has attempted to prove that these elements actually correspond to certain of the horny shields covering the forepart of the head in reptiles, mainly lizards and snakes. The head of these shows a median single shield on the nozzle, known as the rostral (fig. 100, r), and behind this there is, on either side, a series of marginal labials (l); further, a nasal shield, pierced by the nostril, and as a rule two more nasals adjacent to the latter (fig. 100, n). The lower jaw has a single mental shield (m) in front, and a series of infra-labials (il) on the sides. Lönnberg has carefully examined the beak of a great many birds, and in all of them he found, more or less distinct, remainders of the same shields as in reptiles. In fig. 100 we are able to compare heads of reptiles and birds, and by following the lettering, we shall have

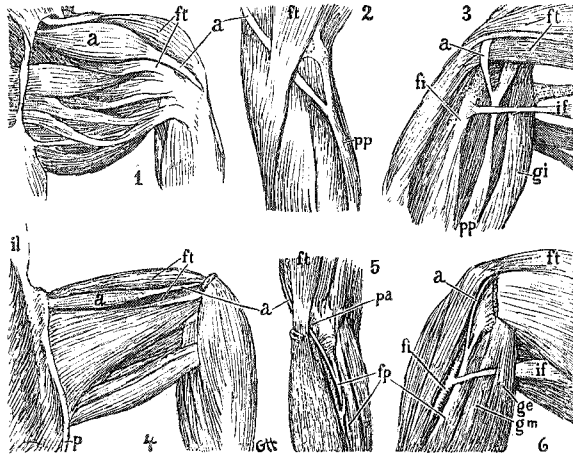


Fig. 99. The ambiens muscle in reptile and birds; 1 and 4 the inside of the thigh, 2 and 5 the knee-joint anterior view by stretched leg, 3 and 6 the outside of hind-leg. 1, 2 and 3 *Alligator mississippiensis* after Gadow, 4, 5 and 6 Black Grouse, *Tetrao tetrix*; a musculus ambiens and its tendon, fi fibula, fp musculus flexor perforatus dig., ft m. femoro-tibialis, ge, gm and gi m. gastrocnemius externus, medius and internus, if ilio-fibularis, il ilium, p pubis, pa patella, pp m. peroneus posterior.

no difficulty in imagining how some of the shields (r and m) of the reptile have enlarged in the bird; others (l and il) have fused together. In the beak of the Cormorant (fig. 100, 7), the number of labials is variable, three or four of these are to be found, but, owing to the reduction of the nostrils, the bird has no nasals. In the Burrowing Snakes (fig. 100, 3—6), the rostral has become enlarged because of its functional importance, just as in the case of birds.

The most striking peculiarity in birds, is their plumage, which apparently has nothing at all in common with the scaly covering of the reptiles. So much more surprising is it, on examining these excrescences microscopically, to learn that the feather is nothing but a further development of the scale.

The first stage of the reptilian scale is a small protuberance occasioned by an increased growth of the cells of connective tissue in the cutis, close to the epidermis (fig. 101, 1). Next arises a small cutis-papilla, covered with

epidermis. This is transformed into a cone (fig. 101, 2), the apex of which is directed backwards, and gradually assumes a flattened shape (fig. 101, 3); further, a pigment composed of asteriated cells of connective tissue, migrating from the cutis into the epidermis (fig. 101, 3, p).

Before the permanent feathers in birds are formed, the down appears. This commences as a group of connective tissue cells in the cutis, on the top of which two thickened layers of epidermal cells are found (fig. 101, 9). Then

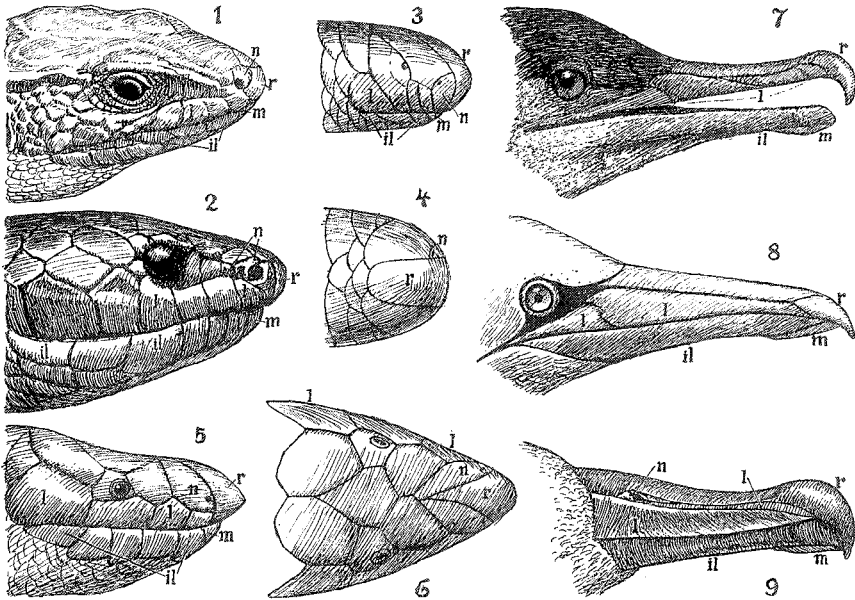


Fig. 100. 1—6 heads of reptiles, 1 Eyed Lizard, *Lacerta ocellata*, 2 Snake, *Rachidelus brazili*, after Brehm, 3 and 4 Blind-Snake, *Glauconia disserta*, after Cope, 5 and 6 Shield-tail, *Uropeltis*, after Boulenger, 7—9 beaks of birds, 7 Cormorant, 8 Gannet, 9 Albatross, 4 and 6 seen from above; il infra-labials, l labials, m mental, n nasal, r rostral.

the cell-group of the cutis grows rapidly, forcing the epidermis outward, and assumes the form of a pimple, called the feather papilla (fig. 101, 10). This is transformed into a cone, the apex of which is directed backwards (fig. 101, 11), just like the scale of the reptile. The cone lengthens into the so-called feather-pulp (fig. 101, 12), and from this pulp the down grows out.

An examination of the scales on the bird's foot, will make this homology between feather and scale still more apparent. Says Kerbert (33), who has studied the development of scales on the foot of the Hen-embryo: "On the seventh day of development we find, exactly corresponding to the second stage of development in the snake, the epidermis consisting of two layers" (fig. 101, 5); uppermost, a layer of flat cells (*epitrichium*), and below, a mucous layer (*stratum germinativum*) of round cells. The horny layer, which is of a later growth, is formed, not from the upper layer, either, but from the mucous layer. "We thus see that exactly the same thing takes place as we

had occasion to observe in the formation of the epidermis of the snake". On the eleventh day does the first beginning of the coming scale appear (fig. 101, 5), and a rapid increase of cells takes place, especially in the cutis. The pimple (fig. 101, 6) thus arising is, for a start, of a regular roundish shape, but from the thirteenth day it begins to bend backwards, and on the fifteenth its flattened structure is plainly distinguishable (fig. 101, 7), so that we are warranted in speaking of an upper and a lower scale surface. "The epidermis

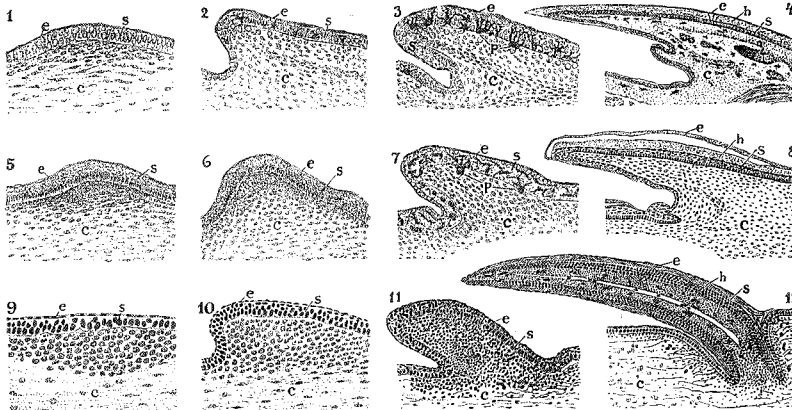


Fig. 101. 1—4 The development of the shield of a reptile illustrated by transverse sections through the skin of 1—3 embryo of Snake, *Tropidonotus natrix*, and through shield of 4 Schelltopusik, *Ophisaurus apus*; 5—8 the development of the shield on the foot of a bird illustrated by sections through the skin of an embryo of Common Fowl, 1—8 after C. Kerbert; 9—12 the development of the feather, 9 and 10 by sections through skin and feather-pulp of an embryo of Pigeon, after Davies, 11 and 12 after Wohlaue; e and s are the two layers of the epidermis, e the external, *epitrichium*, s the inner germinative stratum, below this lies the cutis, h is the horny layer, developed from the germinative stratum of the epidermis, p immigrating pigmental cells.

displays, during this stage of development, still more peculiarities, strongly suggestive of the development of the scale in the snake" (Kerbert, 33). One of these is the appearance of ramified pigmental cells in the epidermis, immigrated, just as in the reptile, from the cutis (fig. 101, 7, p). This is the more striking because these pigmental cells again disappear altogether in the course of development; they are not present in the adult Hen. The development of the scale in reptile and bird, coincides practically from day to day, and on the twenty-third day does the scale on the foot of the Hen-embryo present a decidedly reptilian appearance (fig. 101. 8). The difference between the upper and lower surface, too, is very pronounced, while the scale in the case of the adult Hen, is more buckler-shaped.

Now, the funny thing about it is that, on closer inspection of the scales on the bird's foot, we are witness to the transition from scale to feather. "The entire scale may best be compared to a growing feather, a matter of great importance to the phylogeny of the feather", says Gadow (29). The shank of the bird's foot, in closely related species (e. g. Pheasant and Black Grouse),

may, as a matter of fact, be either scaled or feathered, and the feathering may even extend to the claws (fig. 102, 7). The foot of the Struthious birds, too, may pass all the transitional stages from scale to feather. The transformation takes place as follows: From a scale with a broad base, one part rises above the rest, forming a process, directed backwards. The horny sheath at this place thickens, and small pimples arise, making the edges of the process dentated. On and about each of these pimples does the epidermis grow out, as a number of short, horny processes. Even the flat shape of the scale changes into a more roundish one. From this arises the down.

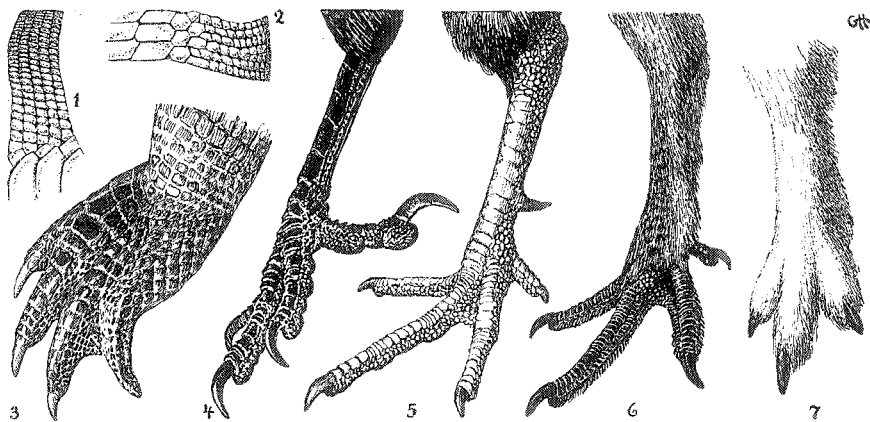


Fig. 102. Shields of 1 Green Lizard, *Lacerta viridis*, 2 Viviparous Lizard, *L. vivipara*, both after F. Leydig. Foot of 3 Alligator, 4 Hooded Crow, *Corvus cornix*, 5 Pheasant, 6 Black Grouse, *Tetrao tetrix*, 7 Ptarmigan, *Lagopus mutus*.

The feather may be considered as a cylindrical, fringed scale, and yet there seems to be a difference in their respective formations, the feather-papilla from which the feather originates disappearing again, while the cutis-papilla of the scale remains intact through life. According to investigations by Kerbert (33), however, it does not disappear in all birds, but persists in the Penguins, the scale-like feathers of which have no shafts, but consist of innumerable conerescive barbs. On the foot of the birds, however, this papilla may be considered permanent, as a feather may evolve from the scale. Now, however, Davies (34) has pointed out that the scales on the bird's foot owe their origin to featherlets, and so he thinks that, morphologically, they are to be distinguished from reptilian scales, which are primary formations, while the bird's scales must be ranged with secondary formations. This seems sound logic enough, but the two kinds of scales, as seen above, correspond in embryonic development and microscopic structure, so there can be no doubt as to their perfect homology. Moreover, it seems to me that Davies's discovery rather indicates that Nature may even furnish a counter-verification of the correctness of our conclusion, showing that not only may scales grow into feathers, but the feather may even turn into a scale once more.

SUMMARY

Let us sum up the results arrived at in Part III:

The temporal hole found in some recent birds, we are not entitled to homologize with the supratemporal fenestra in fossil reptiles.

We have seen nestlings with claws on their fingers like *Archaeornis* and, their foremost primaries being retarded, they will climb, reptile-fashion, the branches of trees.

A patagium between the arm and the trunk, is still to be found in birds.

The entire brain of the bird, in all its main features, is exactly the same as that of the reptile, and, like the eye, it is but a little further evolution of the peculiar characters already found in the reptile. Most striking is the development of the lens, being identical in the two classes.

The same thing was found in regard to the ear, disclosing a wide gap between the mammals and the Sauropsida.

The male genital organ, and its entire development, presents no differences in birds and reptiles, while through the exhibition of the secondary sexual characters, we feel the rhythm of great harmonies.

The preformation of the lungs is nearly identical in both, and the different stages of their development suggest the phylogenetic origin of the lungs.

The ambiens muscle in birds is an inheritance from the reptile.

The separate pieces of the horny sheath of the beak in birds correspond to several of the horny shields covering the forepart of the head in reptiles.

In their development, the feather and the scale are exactly alike, the feather being a cylindrical, fringed scale.

Taken together with the demonstrations in Parts I and II, these points of resemblance furnish striking evidences of the close relationship between the two classes, and with these in mind we are, in Part IV, to look for the group of reptiles from which the birds may have originated.

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PART IV

THE PROAVIAN

INTRODUCTION

IN Part I we made two mental excursions to the unknown regions of past periods, the first one to the Jurassic to view the scenes of *Archaeornis*, while during the second we accompanied a *Hesperornis* couple to the depths of the Cretaceous seas. It was chiefly the outer life and habits that engaged our attention, but in this part we shall try to sound the depths of animal life in its inner bearings.

This will prove to be an exploratory expedition of quite a different character. We shall meet with but few tracts plainly visible to the eye, a good many things will be shrouded in a veil of obscurity, and still more hidden to view in impenetrable darkness, where it will not even be possible to conjecture what particular path to strike.

If this were not the case, we should be absolutely sure of reaching our goal; as a matter of fact we are sufficiently equipped for this expedition and furnished with the general direction of the road leading to same.

Before setting out on our journey, however, we shall review our equipment, so as to have each detail at our disposal when needed. Fortunately, we possess an excellent searchlight, a strong holophote, to pierce the darkness before us. The radiance emanating from the entire bony structure of the oldest birds, be it noted, not merely proves that it is among the fossil reptiles we are to look for the point of departure in regard to the bird-stock, but it also points to definite groups within these. It is but desultory particulars, however, of which now and then we catch a glimpse; the great facts are swathed in obscurity.

The skull of *Archaeornis* proved to be so markedly reptilian as to make us conclude that it would better fit a reptile than a recent bird. The most birdlike features of it, the large orbit and the preorbital fenestra, were present in several fossil reptiles as well. We saw from fig. 5 that the individual bones of the skull had exactly the same position and nearly the same form as in the two Pseudosuchians. The entire quadrato-jugal bar did not at all resemble that of a recent bird, but far more the corresponding one of the Pseudosuchians. The presence of a sclerotic circle and of teeth in distinct sockets, too, were features they had in common. In the bird-embryo there is still a preformation of a tooth-ridge in both upper and lower jaws, and traces of lips are found. The lower jaws of bird and reptile resembled each other considerably, and, in describing *Hesperornis*, we found that they might even be practically identical. The suspension of the lower jaw by means of a quadrate, too, was a common feature of both. The embryonic development, moreover,

went to show that "the embryonic bird's skull is characterized by a wealth of distinct bones that is absolutely reptilian". No new formations in the skull of *Archaeornis* were found to distinguish it from that of the reptile; the braincase itself was probably somewhat bigger in the bird, but this indicated no essential difference. In Part III we saw how wholly reptilian was the bird's brain in the Cretaceous, and even the bigger brain in recent birds, when compared to the reptile, suggested a difference in degree only. The structure of cells in the cerebrum, as well as the tripartition of the cerebellum, was thoroughly reptilian.

The similarity of the outer organs of sense in the two classes was particularly amazing, because it proved to be greatest where least expected. The entire build and development of the eye were identical; colours were apprehended in the same way; their lens had a peculiar form with an equatorial ring not found in the other classes; accommodation was similarly produced, differing from that of the mammals. The ciliary and iris muscles were cross-streaked in the Sauropsides only. In form and structure of the nasal cavity, too, they constituted an exception. The same thing holds good of the build of the ear, a fact which, together with the transformation of the visceral arches, left a deep gap between birds and reptiles on the one hand, and mammals on the other, the ear-ossicles of the latter corresponding to the quadrate, articular, and angular bones of the Sauropsides so that the entire lower jaw of the mammals correspond to only the dentary bone of birds and reptiles.

The notochord offers very strong points of similarity in the two classes. The development of the vertebral column of birds runs parallel with that of the reptiles. Several fossil reptiles have biconcave vertebræ, and so have bird-embryos, *Archaeornis*, and *Ichthyornis*. The bird-embryo, just as well as recent reptiles, has but two sacrals, and may have preformations of as many as 19 caudal vertebræ; moreover, the preformation of the caudal part of the notochord is too long, — all of which, taken together with the long and slender tail of *Archaeornis*, are features unmistakably pointing to the reptile.

Both reptiles and birds have cervical ribs. The development of the thoracic ribs runs parallel in both, and the ventral ribs in *Archaeornis* were found to be an especially reptilian feature.

The sternum in the bird-embryo is preformed in two halves, and so we find it in fossil reptiles. Its development is entirely homologous in the two classes, and the same thing may be said of the shoulder-girdle. This is especially noteworthy in the case of the clavicles, as these bones, fusing into a furcula in the adult bird, look so different from those of the reptile. In their preformation they are for both classes quite separate, they ossify directly from the membrane and never show any trace of cartilage. In both the bird-embryo and in fossil reptiles the clavicle has an attachment to the scapula. A supra-scapula as in fossil reptiles is found in the the embryo of the Hoatzin. So also the reptilian episternum has been traced in bird-embryos.

The preformation of the limbs is alike in reptiles and birds. Though the

fore-limb of *Archaeornis* supported a wing, the carpus was very far from that of a recent bird and in reality the same as that of the reptile; in the hand the whole reptilian basis is still preserved. The metacarpals and the digits are the same, and each one of the digits has the same number of phalanges as those of the reptile; they all wear claws. The bird-embryo has 7 carpals and a preformation of 4 metacarpal rays.

The three pelvic bones are preformed in exactly the same way in the two classes, and the most remarkable thing about it is that the pubis in its preformation is directed forward in both. The pelvis of *Archaeornis* was but small, and its individual and quite separate bones very reptile-like; its sacrum was composed of fewer vertebræ than in many fossil reptiles. There was no pectineal process in the primitive bird-pelvis; it is no doubt a later acquisition, belonging to ilium, not to pubis. In the embryo it develops as a cartilaginous outgrowth of the ilium and ossifies from the latter, not from an independent centre.

In the hind-limb the correspondencies are particularly striking. The fibula is preformed in bird-embryos in exactly the same length as tibia, and in *Archaeornis* it appears fully developed as in reptiles. Among the tarsals the fibulare is a distinct bone in *Archaeornis*, it has not fused with fibula. Besides, Petronievics (34) has found a tibiale and a distinct intermedium, which latter in *Archaeopteryx* ascends the anterior face of the distal end of the tibia, a reptilian feature (fig. 109, C). Each of the distal tarsals seems to have fused with the proximal end of the corresponding metatarsal. The three metatarsals lie separate beside each other and in the same plane exactly as it might be found in the Coelurosaurs. The whole character of the toes, too, their shortening and the proportion in size and number of the particular phalanges, was conspicuously alike in the Jurassic birds and the fossil reptile. The foot of the bird-embryo is preformed as five rays just as in reptiles.

The embryonic development showed us, moreover, that a great similarity subsists between sperm-cells of birds and reptiles, in contradistinction to those of mammals. The preformation of the ovary and the formation of the ovum were exactly alike in the two classes. The similarity in the cleavage of the ovum and in the formation of the ectoderm, entoderm, and mesoderm was very considerable; there was practically no difference at all. The primitive streak, in composition and significance, is entirely homologous in birds and reptiles.

The homologies of birds and reptiles, in the blood-vessels of the yolk-sac, are very pronounced. The thin embryonic sacs, amnion and serosa, are alike in both, while the mammals, on the contrary, have a placenta instead. During the further development of the ovum does the head-process in the bird-embryo correspond to the neural groove in the reptile-embryo; the neural folds and the three ventricles of the brain are developed in the same way; and so are the somites. During the entire period of subsequent embryonic development, the various points of resemblance turned out to be very remarkable; the development of the head was exactly alike in both.

The embryos of the Sauropsides present striking points of resemblance in the development of nearly all organs, e. g. the mouth, the tongue, the Jacobson's-Organ, the thyroid and thymus glands, the intestinal canal, the liver, the spleen, the kidneys, the heart, and the blood-vessel system.

The lungs are preformed in quite the same way, and the lung of the reptile develops exactly along the same lines as in the bird-embryo. Even the air-sacs of the birds are foreshadowed in the lung of the reptile.

The development of the digestive organs is homologous in the two classes. Likewise does the penis, in development as well as in general build, present remarkable common features. In the display of secondary sexual characters, the harmonies are singularly pronounced, in all probability owing to the similar structure of brain. Birds and reptiles have no diaphragm corresponding to that of mammals. The ambiens muscle is a distinctive feature of the Sauropsides. The composite character of the side of the beak in birds may be directly homologized with the corresponding parts in reptiles. Microscopic investigations of scales and feathers go to prove that the feather is nothing but a further evolution of the scale; and not only may the scale become a feather, but the latter may once more become a scale.

From this recapitulation of the points of resemblance subsisting between reptiles and birds, we learn that the homologies are found, not merely in some details only, but may be traced through all parts of the organism and throughout the entire development of same. In many organs, moreover, we found these harmonies singularly striking.

We can therefore with absolute certainty maintain that the birds have descended from the reptiles. Of this we cannot, in future, entertain the faintest shadow of a doubt.

During the unnumbered millions of years that the reptiles were the lords of the earth, their great number and their multifarious forms swelled enormously, and although but a small fraction of what the earth conceals in her bosom has as yet been brought to light, we already know so great numbers that they comprise more than 20 orders and numerous sub-orders, families, genera, and species. Of these, all contemporaries of the Jurassic birds, as well as those succeeding these, are of course excluded from being the ancestors of the birds. When nevertheless some of these figure in our discussion, it is because the forerunners of these reptiles in previous periods are not sufficiently well preserved, and because from forms belonging to later geological epochs it is possible to draw certain conclusions respecting the build of earlier forms.

Besides, all the more specialized forms, as e. g. Ichthyosaurs, Plesiosaurs, Tortoises, Snakes, etc., are of course out of the question, in as much as an organ, for instance, which has evolved into a paddle or is entirely wanting, cannot, as a matter of course, become a feathered wing.

It is to this end that Louis Dollo's (1) ingenious law of irreversible evolution, preferred already 1893, must serve as our guide. The law, since its first appearance, is confirmed by numerous fresh evidences, showing that it holds good in a very large number of cases. But whether it is always valid is

doubtful. The known phylogenetic series, however, point decidedly to the conclusion that any form of reversibility is quite exceptional. O. Abel (2) has worded this law as follows:

1. An organ reduced during the phylogenetic evolution, will never again attain its original structure and function; an organ, entirely lost, can never be regained.

2. If by adaptation to a new mode of life (e. g. by transition from walking to climbing) any organs be lost which by the former mode of life were of a high practical value, these organs, on a return to the old mode of life, will never reappear; in their place, a substitute of other formations, morphologically different, but functionally equivalent, will originate.

Some examples may best serve to illustrate this law. The Jurassic birds had, as we have seen, 20—21 lengthened caudal vertebræ and a leaf-shaped tail. But in the course of evolution this must have proved to be inconvenient, for the vertebræ have been greatly shortened, and some of them have fused into a pygostyle, as a result of which the supporting organ for the feathers became so short that the tail assumed the shape of a fan. Some birds, however, once more required a long tail, and although there were still a good many caudal vertebræ at disposal (in the embryo no less than 19), these could no more lengthen because they had dwindled too much. So the feathers had to grow longer instead, and to this is due the long tail of the Magpie, some Cuckoos and Parrots, the Kestrel, the Kite, and the Pheasant.

The oldest birds had teeth, but these, being no longer needed, were gradually lost, and the jaws were covered with horny sheaths. The London Clay of Sheppey has supplied some remains of an extinct bird, *Odontopteryx toliapica*, which has evidently been missing its teeth, for bony denticles have been evolved from the ridges of the jaws; the teeth that were lost, it would no more have been able to recover. The existing Mergansers have also serrated jaws, and so has the Plant-Cutter (*Phytotoma rara*) of Chili.

From figs. 18 and 19 we saw how the reptile-hand, originally five-digited, in the course of time was reduced by loss of phalanges and metacarpals, so that finally only the three first digits were left, as in the case of *Archaeornis*. It would never be possible to replace these lost digits; the hand cannot revert to its original state, even though later on these very digits should prove to be greatly needed. In a single order of birds, the Penguins, the wing does no more act as such, being transformed into a paddle. In the case of Ichthyosaurs and Plesiosaurs we know how paddles evolved from originally five-digital reptile-hands, by adding digital rays and also phalanges, thus increasing both length and breadth of the paddle. But in the original wing of the penguin, only remnants of three digits were left, and such an increase, therefore, has been out of the question. The adaptation has taken place by a broadening and flattening of the bones present, and all joints, excepting the shoulder-joint, have become immobile. The result, then, is a further specialized form, a more advanced reducing process, and no new formation.

Moreover, we are justified in concluding that the birds cannot have descended

from reptiles wanting any of the bones possessed by the original birds. Thus, the shoulder-girdle or the pelvic arch must be without defects. Several orders of fossil reptiles have no clavicles, for instance, and this in itself precludes the possibility of their being the ancestors of the birds.

When strictly adhering to this law, we shall find that only a single reptile-group can lay claim to being the bird-ancestor, but in order better to explain the existing kinship, we shall proceed to examine Pterosaurs, Predentates, Coelurosaurs, and Pseudosuchians.

PTEROSAURS

The Pterosaurs are of interest chiefly because they are flying reptiles. They furnish a demonstration of the great transformation which the skeleton of the reptile is capable of undergoing in adapting itself to locomotion in the air, but the points of resemblance to those of the bird are in reality rather superficial.

The skull (fig. 104, 3) has elongate and pointed jaws like the bird; there is a sclerotic circle in the orbit; the teeth constitute a single row in distinct sockets, but are longer and more heterogeneous than in the case of *Archaeornis*. The youngest forms from the Cretaceous period show the same tendency to toothlessness as the birds. We saw from fig. 88 that the brain of a Pterosaur might very much resemble that of the most ancient birds. The build of the skull is for lightness, if possible, carried even further than in birds, and the cranium of *Ornithodemus*, for instance, consists of so slender rods that C. Wiman (3) very aptly designates it the ideal of a bicycle-frame. On comparing the cranium of a Pterosaur from the Upper Lias (Lower Jurassic) with that of *Archaeornis* (Upper Jurassic) we have no difficulty in seeing that some of the points of resemblance are, broadly speaking, due to reptilian affinities on the part of the cranium of *Archaeornis*, but the differences, on the other hand, are so profound that no descent is possible.

The shape of the jugal is very peculiar, and the very strange position of the quadratojugal, characteristic of the Pterosaurs (4), is in itself sufficient to remove these considerably from the birds. After Wiman (3), the Pterosaurs have no infratemporal fenestra, and the hole which has hitherto been named so, is in reality a quadrate foramen, the quadratojugal forming the greatest part of the anterior border (fig. 104, 3), while in the Diapsida this is never the case. Neither is the lower jaw much like that of the bird, and even though there are similarities in the palate (fig. 134), the differences are far greater. The bones of the Pterosaurs were pneumatic, just as those of the birds.

The shoulder-girdle has no clavicle, and so the birds cannot possibly descend from these reptiles. Similarities in shape of scapula and coracoid may be quite considerable, and the angle between same may correspond to those of recent birds. The keeled sternum (fig. 103) has attained a strange development, having entirely lost any resemblance to a reptilian sternum, which latter never shows the slightest trace of a median keel. On the dorsal side of this keel

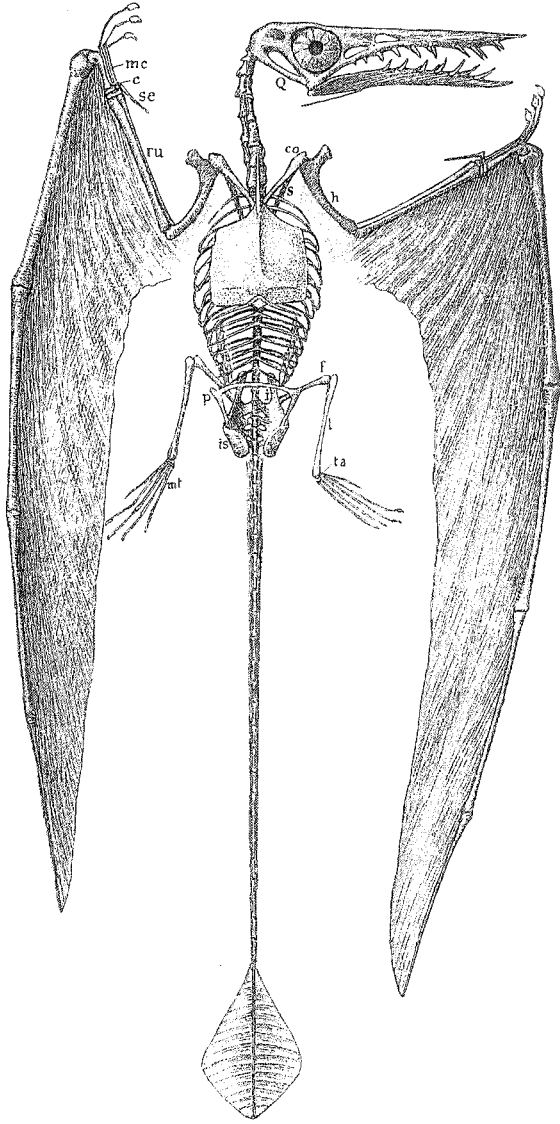
Fig. 103. Skeleton with the wing membranes preserved of *Ramphorhynchus gemmingi*, reconstruction by E. v. Stromer; c carpals, co coracoid, f femur, h humerus, i ilium, is ischium, mc metacarpals, mt metatarsals, p pubis, ru radius and ulna, s scapula, se sesamoid bone, t tibia, ta tarsals, Q quadrate.

lie two coracoid grooves obliquely behind each other (104, 1), the foremost groove receives the right coracoid. In some groups of birds, certain Tubinares, Steganopodes, Storks, Herons, etc., the coracoid grooves overlap widely across the median line, the right one lying ventrally upon the left, as seen in *Ichthyornis* (fig. 104, 2). It is a curious example of an analogous adaptation. The sternum most resembles that of the Cormorant and the Gannet, which is in perfect keeping with the pelagic habits of the Pterosaurs.

Ventral ribs are developed in Pterosaurs as in *Archaeornis*. Their pelvic arch is quite different from that of a bird, but we meet with an evolution of same, analogous to that of the birds, for in early forms (*Dorygnathus*, *Campylognathus*) so primitive conditions still prevail that ilium has not yet fused with the sacral vertebræ, nor these mutually (3), while in the later Cretaceous forms we find as many as 10 vertebræ enclosed in the sacrum, and all the elements of the pelvis fuse to a still greater extent than is the case in recent birds.

Nor do the weak hind-limbs resemble those of birds; only the reduction of the distal end of the fibula presents some resemblance to that of recent birds, *Archaeornis* having a well developed fibula.

The hand, however, is the part of the skeleton most at variance in build, for it has not a shadow of similarity to that of a bird. The hand of *Archaeornis*



has lost the fourth and fifth digits, the first three digits only being present, but just these three digits are in the hand of the Pterosaurs rather rudimental (fig. 103), while the fourth digit is so strong and powerful that it is entirely beyond the bounds of possibility for this very digit totally to disappear and for the three rudimental ones to grow into a bird's hand.

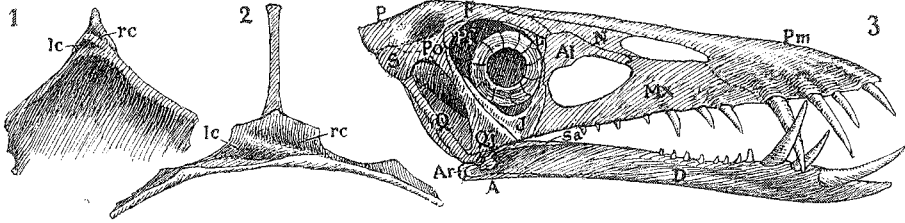


Fig. 104. 1 Sternum seen from behind (dorsal view) of *Campylognathus liasicus* after C. Wiman; 2 sternum, anterior view, of *Ichthyornis dispar* after Marsh; lc groove for left coracoid, rc groove for right coracoid. 3 Skull in profile of *Dorygnathus banthensis*, from the Lias, after C. Wiman and G. Arthaber; lettering as in figs. 3 and 5.

The origin of the Pterosaurs seems to be far removed from the stock of birds, and the various points of resemblance are merely due to adaptations for the flying purpose. But we do learn from these, in how far the skeleton of a reptile may be susceptible to profound transformations, so that large parts may be said to have lost their reptilian character, while others have kept it intact. Hence, we have no difficulty in imagining that, from a still more favourable point of departure in the stock of reptiles, creatures may have sprung capable of changing into forms in every respect far beyond those of the reptile-type.

PREDENTATES

When on our expedition of discovery we meet with the peculiar reptiles to which the above name applies, also called Ornithopoda or Ornithischia, owing to their supposed resemblance to birds, we find, unfortunately, that they almost exclusively comprise forms dating from periods contemporary with or later than *Archaeornis*. Thus, *Camptosaurus* from the Upper Jurassic, *Iguanodon*, *Hypsilophodon*, and *Trachodon* from the Cretaceous. For this reason alone they cannot be the ancestors of the birds.

And yet, mostly on account of their pelvis, there has been an animated and interesting discussion as to the descent of the birds from these very forms. Most authors are of opinion that "the ornithischian pelvis is quite suggestive of that of a bird", to quote one of the most lenient expressions among these.

Before proceeding, we take out one of the books accompanying us on our expedition. The title is "Extinct Animals" (London 1909), and, on opening it we happen to catch sight of a rather astonishing passage, p. 202: "In fact it is now certain that reptiles similar to the *Iguanodon* were the stock from which birds have been derived, the front limb having become probably first

a swimming flipper or paddle, and then later an organ for beating the air and raising the creature out of the water for a brief flight. From such a beginning came the feather-bearing wing of modern birds”.

Dear me! how evident! we exclaim. The origin and evolution of the entire class of birds presented in a nutshell, and not the slightest doubt as to the correctness of the conclusion: “In fact it is now certain”. Hands off! All further investigations superfluous; we may just as well pack up again.

But are we really justified in relying upon our authority? we muse, turning to the title-page, bearing the author’s name. We are struck with awe as we read: “E. Ray Lankester, M. A., LL. D., K. C. B., F. R. S., Late Director of the Natural History Department of the British Museum; Correspondent of the Institute of France”. And in the preface we further read: “This volume is a corrected shorthand report of the course of lectures adapted to a juvenile audience given by me at the Royal Institution, London”.

Well, then there can be no doubt whatever. No scientist, of course, would tell anybody, especially young people, what was not absolutely reliable. A pity, though, that he has not furnished us with an illustration, too, of this interesting process of evolution; it would have been a grateful task to draw the reptile “similar to the *Iguanodon*”, standing half-way in water, waving its paddle-like organs in the air, “raising the creature out of the water for a brief flight”.

We shall merely look a little further into the scientist’s arguments leading to so sweeping a statement. We read as follows: “The foot was very much like that of a bird and had only three toes, and the bones of the pelvis or hip-girdle are extraordinarily like those of a bird”. That is all, and it does not exactly carry conviction as reliable evidence, for both the Jurassic birds have four well developed toes, so they can hardly have originated from a reptile with only three. Moreover, the fore-limb is said to be only “a paddle”, and it is a well-known fact that the transformation into such an organ always implies a pronounced specialization in some definite direction; hence, it can hardly once more change into something so different as a wing. No mention at all is made of the skeleton of the fore-limb as such, although it is, above all, the wing that makes the bird a bird. On the other hand, the author furnishes us with an illustration of the skull of *Iguanodon*, which seems as far as possible removed from that of a bird.

Thus it would, nevertheless, be quite interesting to test the comparison between the Predentates and the Jurassic birds, with the latter of which we have made ourselves so familiar. Possibly we shall arrive at the same conclusion as our eminent scientist; yet it would be instructive and more convincing, within the bounds of possibility, to institute a comparison of the individual bones.

We start with the skull, and inasmuch as *Iguanodon* represents a strongly specialized type, I have, in fig. 105, further drawn the cranium of *Camptosaurus*, the skeleton of which, compared with that of *Iguanodon*, on the whole, shows a more generalized structure. The skull of *Iguanodon* seems to combine

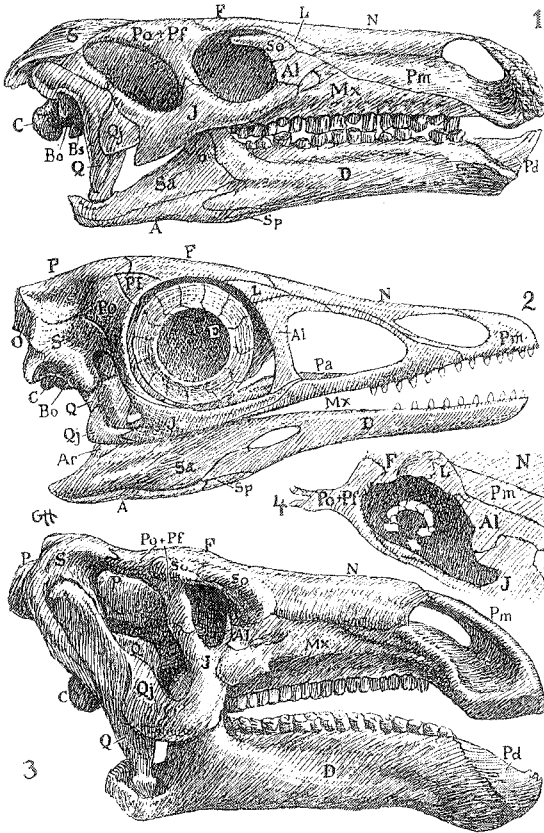


Fig. 105. 1—3 Skulls in side view of 1 *Camptosaurus* from the Upper Jurassic of Wyoming, restoration by Ch. W. Gilmore, 2 *Archaeornis siemensii*, restored by the author. 3 *Iguanodon bernissartensis* from the Lower Cretaceous (Wealden) of Bernissart after L. Dollo and from photograph; 4 orbit with sclerotic ring of *Saurolophus osborni* from the Edmonton Cretaceous after Barnum Brown; Pd predentary, So supraorbital; lettering as in figs. 3 and 5.

features which later on turn up in various mammals. It suggests the cranium of a ruminant; it bears resemblances to *Rhinocerinæ*; the zygomatic arch has a downward bend, reminding one of certain *Xenarthra*. The position of maxillary, premaxillary, and nasal, resembles that of *Grypotherium*, the zygomatic arch of which also bends downwards, and viewed from above, the cranium bears marked resemblances to that of *Sus erymanthius* from the

Lower Pliocene of Pikermi; in profile, too, points of similarity are conspicuous: the small orbit, the heavy zygomatic arch turned downwards, the elevated back part of the head.

All these things, of course, are similarities of an exterior kind only, and spell no real kinship, but they do bear evidence of the manner in which their development has taken place: The muscles due to mastication of articles of food, have moulded the form of the skull. And although the individual bones of the skull of the Predentates are placed somewhat like those of *Archaeornis*, their shape and character differ considerably from same, a fact which, by reference to fig. 105, will be obvious enough. These two skulls are, as it were, of quite another stamp than that of *Archaeornis*.

Thus we find that the postfrontal and postorbital are not separate, and in addition there is a supraorbital not found in *Archaeornis*; and *Iguanodon* has even two of these. The quadrate is considerably lengthened, and its rounded head seems to indicate the possibility of a special motion, the lower jaw, in all probability, having been capable of moving back and forth just as in herbivorous mammals. Also the shape of the squamosal, the quadratojugal, and the jugal, is different; a comparison of the parts of *Camptosaurus*

with those of *Iguanodon* seems to show a tendency in another direction than that of resemblance to birds.

A very essential difference, moreover, offers the preorbital fenestra, which is either very small or entirely wanting. The orbit, too, is small, compared with that of *Archaeornis*, and, though a sclerotic ring is present in the genera of *Trachodontidae* (fig. 105, 4), it bears no resemblance to that of *Archaeornis*. We observe from the size of this ring that the eye was much smaller than the orbital opening. The sclerotic plates (fig. 107, A) were double V-shaped, the overlap being in the long axis of each plate along the area of

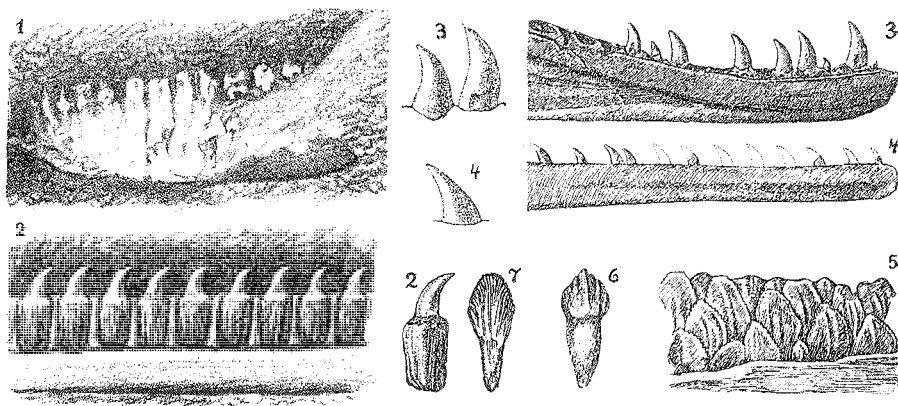


Fig. 106. 1 The dentary part of the lower jaw of *Nanosaurus agilis* from the Upper Triassic of Colorado, showing the dense row of teeth; after F. v. Huene and R. S. Lull. 2 Single tooth and midmost part of the lower jaw of *Hesperornis regalis*, with inner wall of groove removed, showing the teeth in position in the rudimentary sockets, after Marsh. 3 Two teeth and a part of the lower jaw (inner view) of *Plateosaurus cloacinus* from the Triassic, after E. T. Newton. 4 Tooth and inner view of lower jaw of *Ichthyornis dispar* after Marsh. 5 Teeth in the lower jaw of *Iguanodon bernissartensis* after L. Dollo. 6 Tooth from the maxillary of *Hypsilophodon foxi* after J. W. Hulke. 7 Tooth from the dentary of *Camptosaurus medius*, after Ch. W. Gilmore.

the circle, and the outer and anterior border distinctly denticulate (5). They are thus very unlike those of *Archaeornis*.

The high coronoid process of the lower jaw, of a rather mammal-like shape, is another part not found in *Archaeornis*; we see it projecting behind the jugal. And finally, in front of the lower jaw we find an entirely new bone, the chin-bone or prementary (hence the name of Prementates), and a mere glance at the teeth will make it plain to us that these reptiles are considerably removed from the stock of birds.

It may be possible, however, that their ancestors in earlier geological periods had teeth more like those of *Archaeornis*; *Camptosaurus*, we know, is from the Upper Jurassic, and *Iguanodon* from the Lower Cretaceous. Fortunately, a few remains of such an ancestor from the Triassic have been found, viz. *Nanosaurus agilis*, the lower jaw of which is seen in fig. 106, 1. There is no doubt that it belongs to the Prementates, for "behind the last

tooth suddenly rises a steep ascending coronoid process" (6); such a thing, then, was found already in Trias, a fact not suggestive of a bird, either.

A mere glance at fig. 106 will show us how very different, indeed, the teeth of the Predentates are from those of the toothed birds. In *Nanosaurus* the teeth are close together, and their roots extend to the lower margin of the jaw, while in *Hesperornis* the fangs do not reach so far below and are separated by slight projections; in *Archaeornis* they were lodged in distinct sockets and consequently completely separate. The teeth of the Predentates, moreover, were usually placed in several rows, one above another (fig. 106, 5), but those of the birds, in a single row only. Finally, these teeth differ in shape considerably from those of the birds. Just look at Nos. 2 and 7 of fig. 106; in *Camptosaurus* the crown is broad and grooved, while the root is pointed; the toothed birds, on the contrary, have conical pointed crowns, they are smooth and curve slightly backward, and the fangs are large and stout. It is impossible to detect a single point of resemblance.

That the ventral ribs always were wanting in the Predentates, also signify a very marked difference from *Archaeornis*.

A cast of the neural canal in the sacrum of *Stegosaurus* shows an enormous enlargement of the spinal cord in this region, exceeding the mass of the animal's brain more than twenty times. As a lumbar swelling of the spinal cord also is found in birds, it was suggested that this one was an inheritance from the past. In birds the two lateral halves of the spinal cord somewhat diverge, leaving between them a sacro-rhomboidal sinus, filled with a gelatinous substance, thus constituting no real increase of the nervous system. Imhof (7) has now pointed out that this displacement of the spinal cord is a recent acquisition on the part of the birds, making its appearance comparatively late in the life of the embryo, and that it is due simply to a mechanic cause, a pulling of the roots of the great sciatic nerve. The resulting enlargement of the pelvis, however, varies considerably in the individual species of Predentates; in several of these it is wanting entirely, as also in the Theropodous dinosaurs.

If the dilatation in birds really was an inheritance from the reptiles, we should, in the first instance, find it in the oldest fossil birds, but there is no trace of such a thing. All in all, we here have to do with a kind of speculations, the serious refutation of which should really be quite superfluous.

We have already learned that "the bones of the pelvis are extraordinarily like those of a bird", and even so celebrated a scientist as Richard Lydekker, specially trained as a zoologist as well as a paleontologist, says the same thing. In "Harmsworth's Natural History, London 1910", p. 1492, Lydekker calls the Predentates "Bird-like Dinosaurs", and writes: "In the parallelism of the pubis and ischium these dinosaurs resemble birds, and birds alone; and from this and other features it has been thought that the latter are derived from reptiles more or less nearly allied to this group of dinosaurs. But it has to be borne in mind that parallelism has probably played a part in producing this resemblance". Thus it becomes imperative that

these alleged bird-resemblances of the Predentates be subjected to a closer investigation.

In fig. 107 I have, for the sake of comparison, brought together a number of pelvises, and it seems to me that the similarity between ilium of *Camptosaurus* and that of *Archaeopteryx* is very slight indeed (fig. 107, 3 and 5). The postacetabular part in *Archaeopteryx* is pointed and tapering, while in *Camptosaurus* it is the preacetabular part that has this shape; by way of

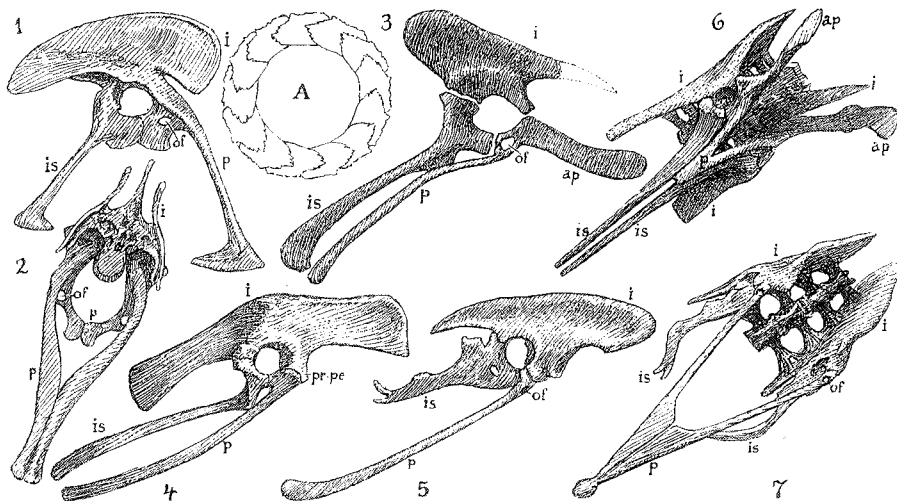


Fig. 107. A Sclerotic ring of *Saurolophus osborni* from the Cretaceous after Barnum Brown, 1 and 2 pelvis of *Ceratosaurus nasicornis* from the Upper Jurassic of Colorado after Chr. W. Gilmore, 1 side view, 2 front view of pelvis and sacrum; 3—5 pelvis in side view of 3 *Camptosaurus medius* from the Upper Jurassic after Chr. W. Gilmore, 4 *Rhea americana*, 5 *Archaeopteryx*; 6—7 pelvis and sacrum in ventral view of 6 *Trachodon* from the Upper Cretaceous, drawn from a photograph of the mounted skeleton, 7 *Archaeopteryx* by the author (see Part I); ap anterior part of pubis, i ilium, is ischium, of obturator foramen, p pubis.

contrast, the part behind acetabulum, in the case of the latter, is broad and rounded.

The ischium does not seem to present the slightest resemblance to that of *Archaeopteryx*, and while the latter, by a considerable lengthening and by disappearance of the various processes, very well might be conceived to change into the ischium we see in *Rhea* (fig. 107, 4), it is impossible to imagine an ischium as that in *Camptosaurus* to assume the same form as that of *Archaeopteryx*. A strongly specialized form cannot revert to the original one. It cannot be denied that ischium in *Camptosaurus* very much resembles that of *Rhea*, but this one is far from being a typical bird. On the contrary, it has lost many features constituting it a genuine bird; thus it has renounced the art of flying. It is a specialized and degenerate type, having struck a path leading away from the character of a bird, a path in which, for instance, *Dinornis* and *Hesperornis* have progressed still further, having almost wholly lost their fore-limbs.

Consequently, it is entirely fallacious to call the Predentates "Ornithischia", i. e. animals with bird-like ischia. Any student of ornithology must enter his protest against making a degenerate type like *Rhea* a representative of the bird-class. Besides, the very name of Ornithischia is a singularly ugly one, which ought to disappear from our vocabulary as soon as possible.

While the pelvis of the Theropoda is triradiate (fig. 107, 1), that of the Predentates is tetra-radiate, the pubis consisting of two branches, the anterior of which (ap in fig. 107) is flat and broad, extending forward, downward, and slightly outward (fig. 107, 6), while the posterior bar lies beneath and parallel to the ischium.

This is the pubis which, in the opinion of most authors, is so extremely bird-like that the derivation of the birds from these reptiles has practically been based on this feature alone. The mere fact that it was directed backward, like that of the birds, has evidently so hypnotized several scientists that they have overlooked, or tried to set aside, the many conspicuous differences between the birds and the Predentates. It is not sufficient to find a single point of similarity, the resemblance ought to be apparent throughout the entire skeleton; otherwise we shall have no right to speak about the derivation of the birds from such reptiles.

The anterior portion (ap) of this pubis, however, was a feature rather embarrassing for this derivation. It was by far too large to be totally ignored, and hence something corresponding to it in the bird-pelvis had to be found. In the so-called pectineal process the desired part was detected by the scientists, who did their best to ignore the fact that this process originated from the ilium, and not from the pubis. In Part I we have already, at some length, made mention of this process and pointed out that it did not belong to the original bird-pelvis, being absent in *Archaeopteryx*, whose corresponding part of ilium is bending a little inward, towards the median line (fig. 107, 7), and further, that embryology proves it to be a new formation on the bird-pelvis, and no inheritance.

We also went into some details as to Lebedinsky's investigations (8), but shall here add what he says with particular reference to the Predentates: "This pectineal process is in Carinates, as for its origin, an outgrowth of the ilium, hence cannot bear any genetic relation to the biradiate pubis of the Predentates, but must rather be conceived as a muscular process of the ilium". And further: "The lower half of the pectineal process of the Ratites (see fig. 107, 4) can represent nothing but a fresh acquisition on the part of the Ratite-pubis".

Even after the publication of Lebedinsky's embryological investigations, an author has maintained the derivation of the birds from the Predentates, taking for granted that this pubis settles the question of kinship. He has managed to illustrate a *Rhea*-pelvis, in which the suture between ilium and pubis is drawn in such a manner that the considerably enlarged, pectineal process looks as if it entirely belonged to the pubis. Then he is able to win at a canter, and after a comparison with the pelvis of *Camptosaurus* he goes into

ecstasies and exclaims: "The connection is downright marvellous" ("Der Anschluss ist geradezu wundervoll"). That the Predentates have neither clavicles nor ventral ribs gives him no trouble at all (8*).

Another author considers it probable that the birds have passed a stage in which they, like the Predentates, had a prepubis, which has disappeared again. He is incapable of sustaining his theory with any palpable evidence whatever, and, as we have seen in Part I, it is refuted by embryology (p. 20).

There are others, however, who are not infatuated with this "bird-like" pubis. Of these I shall only mention what Osborn (9) says: "The primitive (or embryonic) bird pelvis is triradiate and resembles that of the primitive carnivorous dinosaurs. The secondary, or adaptive, bird pelvis is totally different from that of any dinosaur. This militates against the theory of the derivation of birds from any specialized dinosaurs, such as the Iguanodontia, but not against the theory of a common dinosaur-avian stem".

The way in which this pubis has been homologized to that of birds is described by O. Abel (10), as follows: "The pubis of the Ornithischia, backward directed, used to be considered mostly as a new distinctive formation on the part of this group of reptiles, and described as "postpubis", while the pelvic branch directed forward was homologized with the pubis. Consequently, this would have been a case of convergent adaptation, and as such I tried to represent it in my "Paläobiologie der Wirbeltiere" (1912, p. 269). Inasmuch, however, as strong reasons have since then been urged to prove that the anterior pelvic branch of the Ornithischia does not correspond to the pubis, but must be regarded as "processus pseudopectinealis", a new acquirement, while the posterior pubic branch merely represents the former pubis, directed backward even as in birds, we here have to do, not with a case of convergent, but only of a parallel adaptation".

According to this last theory, then, it is the backward directed pubic branch of the Predentates which is the real pubis, forming a symphysis, and it corresponds to the forward directed pubis of the Theropoda, which therefore in the case of the Predentates should have turned backward. I do not think it was quite clear to the advocates of this theory how this turning had been effected. On comparing a pelvis of e. g. *Ceratosaurus* (fig. 107, 1), which has a foramen in pubis, with that of *Camptosaurus* (fig. 107, 3), we shall find that the foramen of the latter has the same position as that of the former pelvis, in its relation to the foremost branch (ap) of the pubis, but this would hardly be the case, if it were the original pubis which had turned backward. It does not seem very likely to me, moreover, that this portion of the pelvis should turn backward, while another element should grow out and take the place of the former. This would seem to be too clumsy a proceeding on the part of Nature. The only thing that apparently militates against this view, is the pubic symphysis. But the portion comprising the pubic foramen in *Ceratosaurus* constitutes in reality also a symphysis, as shown in fig. 107, 2. Hence, it seems much more natural to me to suppose that it is this part, directed backwards and medianwards, of the original pubis which has lengthened posteriorly,

forming the pubis of the Predentates. Its symphysis has been retained, while that of the anterior part of the pubis (ap) has loosened, even as the original pubic symphysis in *Archaeopteryx* has been abandoned in recent birds.

Thus all real resemblance to the bird-pubis would disappear, for the fact that this postulated likeness to birds has produced the fallacious and lengthy name of "processus pseudopectinealis" for this anterior pubic branch, makes no difference whatever. Of course, it is impossible to make out a strong case, until some further finds furnish us with materials to show how this bi-radiate pubis has been evolved. But whether we take one theory or the other, we cannot get rid of the large forward directed branch of this pubis, which has absolutely nothing corresponding to it in the original bird-pelvis (see especially fig. 107, 6 and 7).

As to the cause of the origin of this backward directed pubis in the Predentates, only one opinion obtains amongst authors. They conclude that, as the birds are bipedal and have their pubis turned backwards, the Predentates must have such a pubis as well, because they also are bipedal. Thus, bipedalism should be the primary factor, i. e. the cause of the backward directed pubis. F. v. Huene (11) speaks of "the erect position of the body, which is requisite to the backward turning of the pubis", and O. Abel (10) of "the causal connection between the erection of the body and the formation of a slender pubis lying under the ischium".

I am by no means going to refute the possible correctness of this argument, but, as a matter of fact, it is a very bold conclusion indeed, seeing that a great number of bipedal types have no backward directed pubis, and that some of these, moreover, as e. g. the swift and light-footed Theropoda and Coelurosaurs, in many respects are far more bird-like than the Predentates.

Dollo has gone still further, having arrived at the conclusion that a transformation of this pubis, either by means of a great reduction or by fusing with the ischium into a single bony rod, is due to a reversion of bipedal types into those of quadrupeds. This may be perfectly correct, but it does not seem to harmonize very well with the reduction of the pubis.

If the theory referred to above be correct, it follows as a matter of course that forms which are decidedly bipedal must have a pubis of the same length (or still longer, e. g. *Archaeopteryx*) as ischium, and the more quadrupedal they become, the more the pubis should be shortened. According to this, *Camptosaurus* (107, 3) should be a pronounced bipedal, *Iguanodon* (fig. 110, 1) somewhat less so, and *Trachodon* (fig. 107, 6) the most quadrupedal, the length of its pubis being but a little more than one third that of ischium. According to the statements of the various authors themselves, however, these are not at all the actual facts with regard to these animals.

R. S. Lull calls *Trachodon* "a fine cursorial type" (19, p. 522), and its skeleton is mounted, stretched out for full bipedal speed, in the Yale University Museum. The footprints traceable to *Iguanodon*, into which also its foot fits, bear evidence of a bipedal animal, walking or running, while *Camptosaurus* was evidently far from being a pronounced bipedal animal. Gilmore (12), who has

furnished us with an excellent description of its skeleton, says as follows: "Although there is a considerable disparity in the length between the fore and hind limbs, there appears to be some evidence to show that the bipedal mode of progression was not habitual. While I do not wish to be understood as believing that the upright position was not frequently assumed, still it appears to me that the quadrupedal posture was used more frequently than has been generally supposed. This is shown by the compact, ossified carpus, with smooth, well-defined articulating surfaces, which is supported by comparatively short and stout metacarpals (fig. 116, 8), whose function was that of support rather than prehension. When compared with those of animals whose

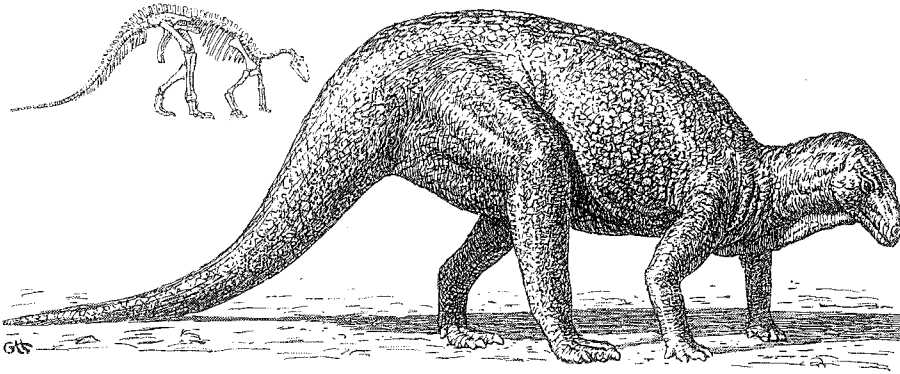


Fig. 108. A sketch of the mounted skeleton of *Camptosaurus browni* in the United States National Museum after Ch. W. Gilmore and a restoration of the same animal by the author.

mode of progression is normally bipedal, the suggestion advanced here becomes apparent. *Trachodon* (fig. 116, 6) has slender, elongated metacarpals and imperfectly ossified carpus, and *Iguanodon* also has a tendency toward the lengthening of the metacarpals (fig. 116, 7), though not so marked as in the former genus. The curved femur is also indicative of a flexed limb, which would have equalized somewhat the difference in length between the fore and hind legs. This character of the femur is in striking contrast to the straight femur of both *Iguanodon* (fig. 110, 1) and *Trachodon*, a provision, as in the Proboscidae, for the support of great weight. The obliquity of the anterior caudal centra indicates a rapid dropping of the tail as it leaves the sacrum, which is also suggestive of a normal quadrupedal position. In the two genera mentioned above the caudals extend straight out from the sacrum without appreciable ventral deflection".

In a subsequent paper (12*) Gilmore has drawn the skeleton of *Camptosaurus browni* in the United States' National Museum. It is mounted in a quadrupedal posture (fig. 108), and from this I have in fig. 108 drawn the restoration of the animal. Gilmore further remarks: "*Camptosaurus* used the quadrupedal mode of progression more frequently than any other known member of the Ornithopoda, and in this genus it may represent the beginning of the development of a fore foot where quadrupedalism was to become a

fixed means of locomotion as it has in *Stegosaurus* and in the *Ceratopsia*". *Camptosaurus browni* is a large clumsy animal, whose entire length was 17 feet; in shape it very much reminds one of the Stegosaur (fig. 123).

On comparing the hand of *Camptosaurus* with that of a quadrupedal mammal, as shown in fig. 116, 8 and 9, we see plainly that *Camptosaurus* made use of its fore-limb to support the body. When nevertheless there is a superficial resemblance between the ischium and postpubis of this animal with the corresponding bones in the Rhea, which is a bipedal fast runner, we can attach no importance to it whatever. A more profound resemblance to the pelvis of *Archaeopteryx* is wanting.

In his "Lebensbilder", p. 359, O. Abel (13) writes as follows: "That a great similarity in the muscular structure must have prevailed between the birds and the Ornithischia is, amongst other things, also evident from the presence of the trochanter quartus in the two groups. The trochanter quartus is a process at the posterior margin of the femur, and it serves the insertion of the musculus caudo-femoralis. This process extends upwards, forming a ridge to which the musculus ischio-femoralis is inserted. The musculus caudo-femoralis originates, in the case of the birds, from the chevron bones of the caudal vertebræ and inserts on the fourth trochanter of the femur, while the musculus ischio-femoralis originates from the ischium, its lower end partly joining the tendon of the musculus caudo-femoralis and partly inserting on the femoral ridge lying above the trochanter quartus. From the presence of the trochanter quartus and the ridge lying above same in the femur of *Iguanodon*, Dollo was able, already in the year 1883, to point out that these muscles, which play an important part for the locomotion of the birds, must have been present in the same development in *Iguanodon*, as well".

And he further remarks (10, p. 614) about this fourth trochanter: "Its presence must be considered an essential feature incident to the erect gait" (Sein Vorhandensein ist als ein wesentliches Begleitmerkmal des aufrechten Ganges anzusehen).

It is very possible that there has been a certain similarity in the position of the above-mentioned muscles of birds and Predentates, but it is just as probable that the disparities have been great, for the development of the fourth trochanter in the two groups has differed considerably. In fig. 109 I have furnished examples for comparison. *Archaeornis* has no fourth trochanter, nor does Marsh refer to any in speaking of *Hesperornis*, but merely says that the shaft of the femur "is marked on the posterior, inner, and outer surfaces by strong prominences for the attachment of muscles" (fig. 34, H). The femur of *Hesperornis* is so strongly specialized owing to its motion in water that it is of no significance in this connection. A bird with an erect gait, however, is *Ichthyornis*, and Marsh says about its femur: "The shaft is slender, and nearly smooth, being destitute of the rugosities seen on the femur of *Hesperornis*". In recent birds the fourth trochanter is mostly very slightly developed. I have drawn the femora of two pronounced gressorial and cursorial birds, *Dinornis parvus* and Common Fowl (fig. 109, 1 and 2). In the first one we

see no trochanter, and Owen does not mention it; he merely points out that "a linear rising or ridge descends along the inner side of the shaft". In the case of the Common Fowl I have had to draw it a little larger than it really is, in order to make it visible at all. The muscles in question are, as far as also the Common Fowl is concerned, rather weak and slender.

The development of the fourth trochanter in *Camptosaurus* (fig. 109, 5 and 6) offers a striking contrast to the above. It is little short of being enormous. Gilmore (12), in referring to same, says as follows: "A compressed fourth trochanter of the pendant type is developed on the postero-internal margin

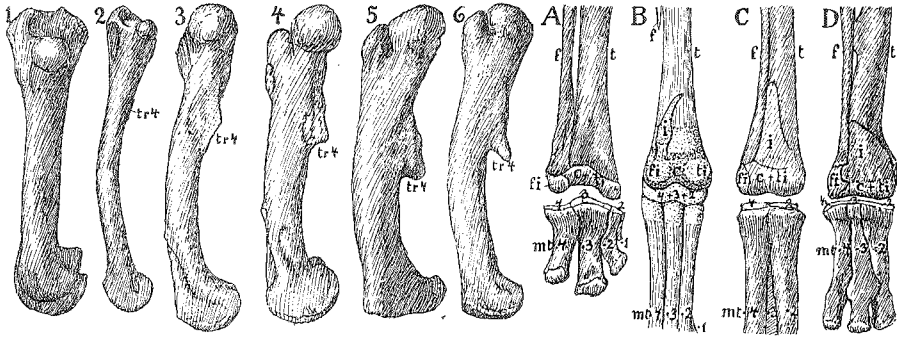


Fig. 109. Left femur, internal view of 1 *Dinornis parvus* from the Pleistocene of New Zealand after Owen, 2 Common Fowl, 3 *Antrodemus valens* from the Jurassic after Chr. W. Gilmore, 4 *Tyrannosaurus* from the Upper Cretaceous after H. F. Osborn, 5 *Camptosaurus dispar* from the Upper Jurassic after Gilmore, 6 *Camptosaurus leedsi* from the Cretaceous after Lydekker; tr4 fourth trochanter. A—D Tarsus, frontal view of A *Iguanodon* after Dollo, B embryo of Hoatzin, *Opisthocomus* after W. K. Parker, C *Ornithomimus* from the Cretaceous after Marsh, D *Tyrannosaurus* after H. F. Osborn; c centrale, f fibula, fi fibulare, i intermedium, mt 4—1 fourth to first metatarsal, t tibia, ti tibiale, 2—4 distal tarsals.

of the shaft", "the apex being directed downward and inward toward the distal end of the bone. Just anterior to the trochanter is a shallow vertical depression with markedly rugose surface which extends out on the internal surface of the trochanter". Besides the femur of *Camptosaurus dispar* I have also drawn that of *C. leedsi* in order to show the difference in development of this trochanter in kindred species.

When further it has been urged that the presence of the fourth trochanter is "an essential feature incident to the erect gait", it is a little unfortunate that *Camptosaurus*, which is as much quadrupedal as bipedal, if not more so, has an enormously large trochanter, while it is but small in the bipedal birds. So also has *Hypsilophodon* a powerful fourth trochanter of the pendant type in spite of the fact that, according to Dollo's theory, it must be secondarily quadrupedal, its pelvis closely resembling that of *Stegosaurus*.

When so great stress is laid on the development of the fourth trochanter in certain Predentates and birds, it is strange that not a word is being said about its presence in the bipedal Theropoda and Coelurosaurs, not quite so powerful, indeed, as in the Predentates, but much more conspicuous than in

the birds. The femora of *Antrodemus* and *Tyrannosaurus*, represented in fig. 109, 3 and 4, show this. In *Ceratosaurus*, the femoral trochanter, after Gilmore (14), is like that of *Antrodemus*. Such a one is found in *Podokesaurus* (15), in *Struthiomimus* (fig. 110, 4), in *Gorgosaurus*, in *Greslyosaurus*, and in *Procompsognathus triassicus* (16) whose "fourth trochanter is a steep ridge, 16—17 mm long and 2—3 mm high", and "laterally, close to the trochanter quartus there is a deep elongated groove for muscle insertion". Of *Anchisaurus colurus* (15) we read: "The fourth trochanter of the femur is prominent", and of *Anchisaurus polyzelus* (15), that the fourth trochanter "is short; inside of it a large rugose surface indicates the insertion of a powerful muscle", hence, the very same thing as we learned of *Camptosaurus*.

It has not been possible for me, I am sorry to say, to make myself acquainted with Dollo's original works, as these are not to be found in our libraries. But O. Abel (13) reproduces an illustration after Dollo, in which the muscles in question are traceable, inserted on the fourth trochanter of the femur of a common Duck. Dollo, it must be admitted, has been fortunate in his choice of the bird, for m. ischio-femoralis is well developed in *Anseres* (Geese, Swans, and Ducks). It is a little rash, however, from this to jump at conclusions respecting birds in general, for the muscle is entirely wanting in several orders.

It also seems rash to speak of "the presence of an essential feature incident to the erect gait", for although we may be entitled to allow the *Anseres* an upright gait, most of them waddle badly. But when we learn that this muscle is still better developed in the Divers (17), what are we to think of the "essential feature incident to the erect gait"? As a matter of fact, not only have the Divers no erect gait, but they cannot walk at all.

On the other hand, the diurnal birds of prey walk rather erect, but this order has no m. ischio-femoralis whatever (17). So also it is rather detrimental to the theory that it is present in some *Limicolæ*, e. g. Curlews, Oystercatchers, and Avocets, while it is entirely absent in Lapwings, Woodcocks, Knots and Dunlins, Sandpipers and Redshanks (17), yet all these birds walk and run perfectly erect.

That these muscles "in the locomotion of the birds play an important part" (13) seems rather puzzling, as so many of the birds have no m. ischio-femoralis at all. We can hardly take it in good earnest, either, when a comparison is attempted between the unknown, but undoubtedly powerful, caudo-femoral muscles of the Predentates with the weak and slender m. caudo-femoralis with which the Ducks wriggle their rumps a little. I think we had better dismiss the possibility of joining together birds and Predentates on the basis of the fourth trochanter and the muscles inserted on same; — at least till some more reliable material be forthcoming.

O. Abel (2 and 13), however, has been struck with the fact that several Theropoda and mammals are bipedal, although they have no backward directed pubis like the Predentates and the birds. He does not from this infer that this pubis possibly may have nothing to do with bipedalism, but merely

supposes that this difference must be due to heterogeneous muscles and certain mechanical causes, surmising that the tail of the former has played a part in locomotion different from that of the latter.

While therefore maintaining that bipedal Predentates have moved about like gressorial birds, he compares the bipedal Theropoda to Kangaroos and Jerboas, supposing that their mode of progression has been saltatory. In a paper, "Die Bedeutung der fossilen Wirbeltiere für die Abstammungslehre,

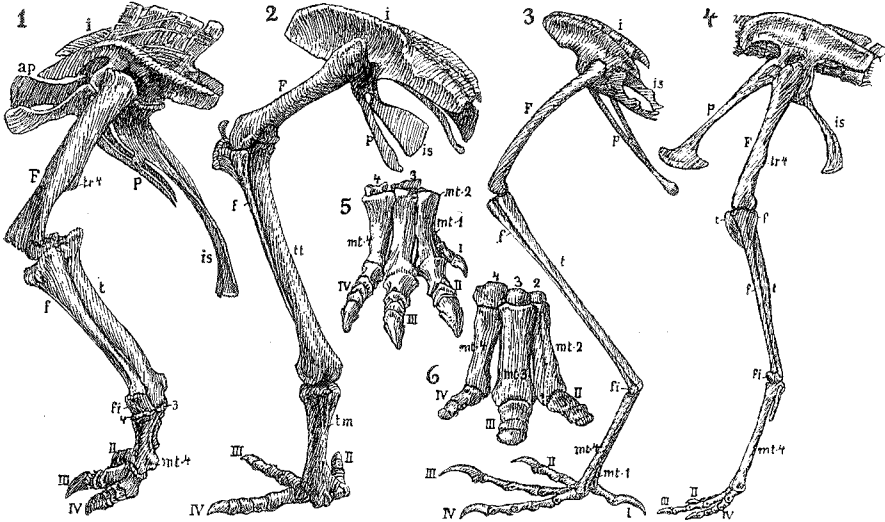


Fig. 110. 1—4 Pelvis and left hind-limb of 1 *Iguanodon bernissartensis* after L. Dollo. 2 *Dinornis parvus* from the Pleistocene after Owen, 3 *Archaeopteryx*, 4 *Struthiomimus altus* from the Upper Cretaceous of Canada after H. F. Osborn; 5 and 6 right foot front view of 5 *Camptosaurus dispar* after Gilmore, 6 *Megacerops tyleri*, a mammal from the Lower Oligocene after E. v. Stromer; F femur, ap anterior part of pubis, f fibula, fi fibulare, i ilium, is ischium, mt 1—5 first to fifth metatarsal, p pubis, t tibia, tm tarso-metatarsus, tt tibio-tarsus, 2—4 distal tarsals, I—IV first to fourth toe.

Jena, 1911", he writes, p. 220, that *Compsognathus* "was a bipedal saltatorial animal which, when jumping slowly, dragged its tail on the ground, but, when leaping faster, carried it stretched out behind to balance the body". Abel concludes his reflections (12), however, very wisely and carefully by saying "that a solution of this question can be rendered possible only by thorough myological investigations".

Without entering further into this difference, therefore, I shall merely point out that a short neck is characteristic of the saltatorial bipedal mammals, while Coelurosaurs are long-necked and Predentates rather short-necked. It is impossible for me to imagine *Struthiomimus* (fig. 132), having a very long neck, progressing saltatorily, just as I cannot imagine an ostrich doing so. The entire hind-limb of *Struthiomimus* (fig. 110, 4) absolutely foreshadows that of a swift cursorial bird.

But the conclusive solution of this problem is the evidence furnished us by the many fossil footprints of bipedal Dinosaurs. R. S. Lull (18, p. 472) says:

"There is no evidence whatever among the footprints of a leaping dinosaur, that is, one in which both feet leave the ground at the same moment".

Let us next return to the wonderful *Iguanodon*-stock, from which we started. It remains for us to examine the foot and fore-limb.

In fig. 110 it is possible to compare the whole hind-limb and pelvis of *Iguanodon* with those of *Archaeopteryx* and of *Dinornis*, a strongly specialized, heavy, cursorial type. Figs. 1 and 2 are nearest to one another; the resemblances between *Iguanodon* and *Archaeopteryx* are but small. Their tarsus has the same character, the joint being in the middle, between the distal and the proximal rows of tarsals, which in the Predentates is closely applied, but not ankylosed, to the tibia and fibula. The two or three distal tarsals are flattened, cushion-like bones, which remain distinct, and never fuse with the metatarsals, as they do in birds. Not knowing what the front view of the tarsus of *Archaeornis* was like, I have in fig. 109, B, shown that of a Hoatzin-embryo for comparison with *Iguanodon* (fig. 109 A). The tarsals of the distal row have already fused together in the bird, and there is an ascending process (i), which is not present in the Predentates. This ascending process Parker has called intermedium, and I think he is right, because in the primitive tarsus this bone is wedged up between the tibia and the fibula (fig. 113, A). As previously mentioned, Petronievics (34) has found this ascending process in *Archaeopteryx*; it is consequently a feature of the primitive bird-tarsus.

This wanting intermedium-process, therefore, marks an important distinction between the tarsals of the Predentates and those of birds, and in this respect the tarsus of the Coelurosaurs (fig. 109, C) and of the Theropoda (fig. 109, D) is much more bird-like, these last having a conspicuous ascending process. Notice also in fig. 126, K the ascending process in the tarsus of the Ostrich.

The metatarsals are somewhat bird-like, but just as much do they resemble those of mammals (fig. 110, 6). As the reptiles have given rise to both birds and mammals, it stands to reason that several fossil reptiles will present mixed features from both of these classes. Thus the toes may be bird-like as well as mammal-like, but the unguals of Predentates are generally of a depressed shape, they may even be rather hoof-like, while the Theropoda and birds have compressed unguals.

This of course is only of inferior significance, because all the Predentates we know are late, strongly specialized, forms, while the skeletons of the limbs of their ancestors in Perm or Trias are unknown. The only means we have of forming an idea of same, is by studying the numerous footprints traceable from more or less bipedal reptiles (fig. 112, A). Several of these have been classed with the Predentates. R. S. Lull (19) writes as follows: "The first known record of Ornithischia is that of their fossil tracks upon the Connecticut valley late Triassic rocks, for with some of the footprints are seen the impressions of smaller hands whose five fingers were armed with rounded claws, like those of known predentates, but totally dissimilar to the grasping claws of a carnivore". This author, who has made a careful study of these footprints,

characterizes them as follows (15, p. 207): "Bipedal dinosaurs, with a mesaxonic, generally digitigrade, tetradactyl or functionally tridactyl foot, armed with more or less blunted claws. The foot ranges from the plantigrade, functionally tetradactyl type of *Otozoum*, through the digitigrade and functionally tridactyl pes of *Anomæpus*. The manus is pentadactyl with blunt claws, and, while occasionally touching the ground in the resting position, is apparently never used for locomotion; it is considerably smaller than the pes. A caudal trace is occasionally present in some genera".

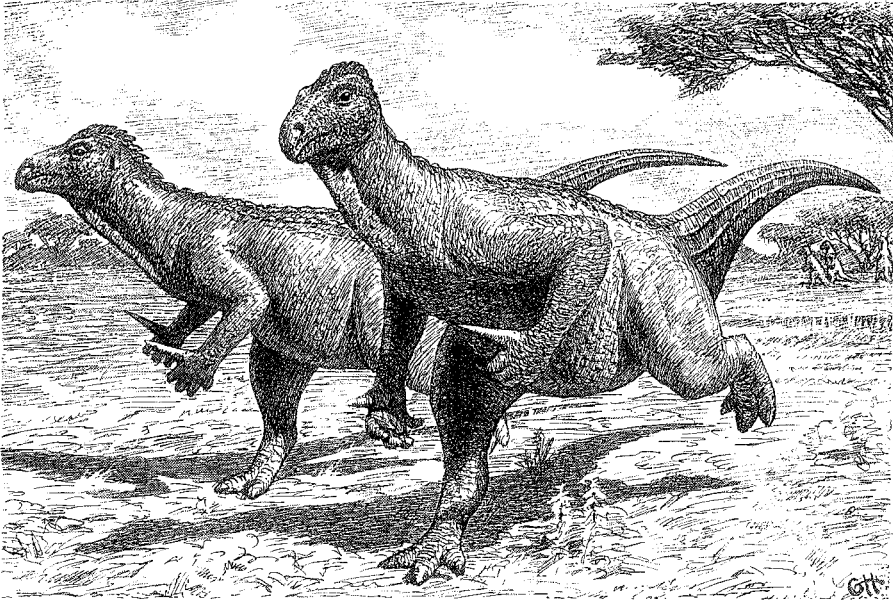


Fig. 111. Restoration of *Iguanodon bernissartensis* by the author.

Otozoum (fig. 113, B) is bipedal with a plantigrade foot and a non-rotated hallux; the hand is relatively small.

The family characters of *Anomæpus* are "bipedal in gait, the manus impressing only when resting (figs. 112, B and 113, C). Pes tetradactyl, digitigrade, with elongate metatarsal segment upon which the animal sits (calci-grade) while at rest. Hallux half rotated, insistent, and subfunctional, but rarely impressing. Pes ornithoid". The genus *Sauropus* (fig. 113, D) resembles *Anomæpus*, but is somewhat larger, has less divarication of the digits and a non-rotated hallux.

Lull's main reason for classing these footprints with the Predentates "lies in the impression of the manus" (15), and I think that he is right in this, but to me it is a matter of rather more vital importance that the first toe is never turned to the rear, as it is in the Theropoda. Thus we are pretty safe in supposing that these footprints belonged to Predentates. That of *Otozoum* is, I presume, the least reliable of them, but, on the other hand, it is so primitive in build that it might be the forerunner of several groups.

R. S. Lull (19, p. 414) very aptly says of these tracks: "The footprints are of double interest, for not only are they oftentimes so well preserved as to enable the student to trace much of the structure, but they sometimes give a clue to the proportions of the entire animal, especially when to the impressions of the hind feet are added those of the hands and tail. Furthermore, the footprints bring before the observer more clearly than any other records of the past the individuality of the creature, for they are fossils of *living beings*, while all of the other relics are those of the dead".

Lull also draws the skeleton of the hand and foot within the footprints reproduced here (fig. 113, B and C), but he institutes no comparison with the

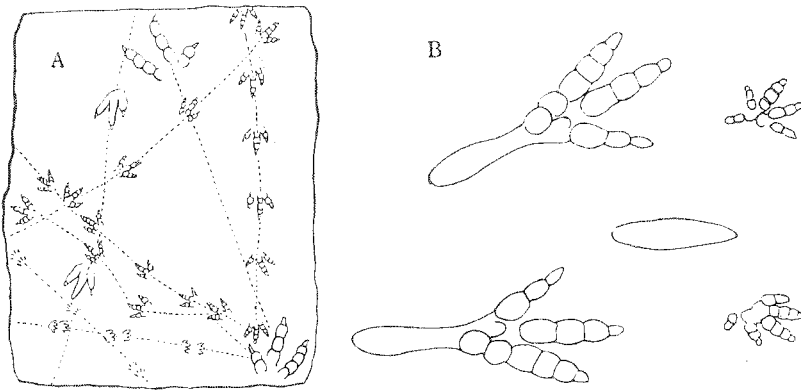


Fig. 112. A Fossil footprints from the Connecticut Trias, Dafter ana; the dotted lines connect the prints made by the same animal. B Impression of all four feet of *Anomæpus scambus*; animal seated; the impression of the breast is seen in the middle.

foot of the known Predentates and that of birds, although designating the former "Pes ornithoid".

This appellation, however, I cannot concur in, and so I shall try to examine it a little more closely, it being a matter of great importance to our research, as far as in any way possible, to understand the foot and the hand of these Trias-Predentates. Now, there is a great difference between fossil bones and fossil footprints, inasmuch as well preserved bones may give us the exact forms, but if these are not found *in situ*, their relative position may often be doubtful. By way of contrast does the footprint show the exact position of the bones, as well as their relative lengths, especially when the impression is made by a seated animal, but the form of the bones, on the other hand, is to be reconstructed from those of kindred animals.

Fortunately, there are traces of the same species, both seated (fig. 113, C) and walking (C₁); fig. 113, D and D₁ even show the same specimen in these positions. The walking pose shows the true position of the toes, and we notice that the first one is never turned to the rear, it touches the ground with the tip of the ungual. The seated pose shows the length of the shank or approximately that of the metatarsals, but not the breadth of these, and

in *Anomæpus* I think that Lull has drawn them too slender, for the light impressions rather show a ridge along the back of the shank and the more prominent portion of the heel; this is plainly distinguishable in the footprints of *Sauropus*, where the middle of the shank has left no impression at all. Likewise, Lull has drawn the upper end of the third metatarsal, thrust back-

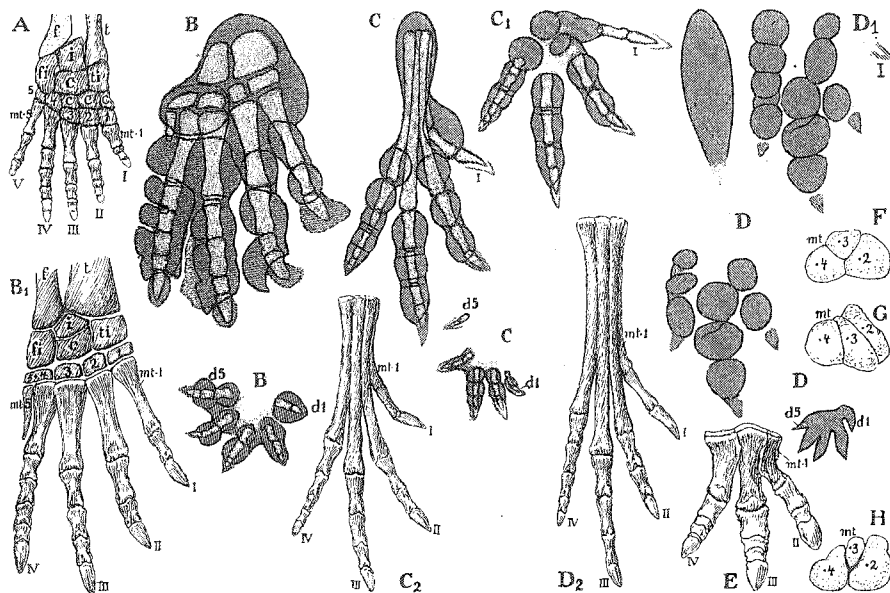


Fig. 113. A Foot of *Trematops*, a Stegocephalian from the Permian after S. W. Williston, to show a primitive tarsus. B Impression of foot and hand of *Otozoum moodii* with the supposed skeleton drawn in, after R. S. Lull; B₁ the skeleton of same isolated; C impression of foot and hand of *Anomæpus intermedius*, animal seated, C₁ footprint of same, animal walking; the supposed skeleton drawn in, after R. S. Lull; C₂ the skeleton of the foot of same isolated; D impression of foot and hand of *Sauropus barrattii*, animal seated, D₁ footprint of same, animal walking, after R. S. Lull; D₂ the skeleton of the foot of same reconstructed; the footprints are all from the Connecticut Trias. E Foot of *Iguanodon* after Dollo. F—H Superior aspect of metatarsals (2—4) of F *Dinornis elephantopus* after Owen, G *Iguanodon* after Dollo, H *Ornithomimus velox* after Marsh; lettering as before.

ward much more than in *Camptosaurus* and *Iguanodon*. Whether the fifth metatarsal were present (as in *Hypsilophodon*) we cannot, of course, see from the footprint.

In the three foot-skeletons which in fig. 113, B₁, C₂, and D₂ I have isolated from the footprints, I have, for the above reasons, made the bones considerably heavier, and also because the metatarsals of *Camptosaurus* and *Iguanodon* are short and stout. And yet, we are surprised at the length of the metatarsals and find it difficult to imagine that these should first have lengthened considerably in Trias and, later on, in Jura and Cretaceous again have been greatly shortened. *Sauropus* may easily be derived from *Anomæpus*, but this does not seem possible to me in the case of *Camptosaurus* and *Iguanodon*.

The three long metatarsals are somewhat suggestive of those of saltatorial and cursorial mammals, as for instance *Eohippus*; we are also reminded of the lightly built, slender, cursorial rhinoceroses such as *Hyracodon*, which have become extinct, while the extant clumsy forms survived them. This finds its parallel in the terminal forms of the Predentates, the heavy and awkward Stegososaurs and *Ceratopsia*.

It is also interesting to observe that the evolutionary process of the foot advances that of the hand, for it confirms what the footprints tell us: that the foot has been the main propelling organ, and therefore the first to feel the influence of cursorial adaptation, resulting in the loss of the fifth digit and the shortening of the first metatarsal, while the hand, as in *Iguanodon* (fig. 116, 7) has retained the complete number of digits. It is the very opposite in the case of the birds, where it is the hand that has been subjected to the greatest reduction. The three long metatarsals, with their distal parts, also seem to divaricate considerably more than in birds; that this is no mere coincidence, will appear by comparing the metatarsals of *Iguanodon* (fig. 113, E).

All in all, we may say that the foot of these Trias-Predentates did not at all resemble that of the birds, as proved conclusively by the position of the first toe. As a matter of fact, it is no "hind-toe", like the hallux of the birds, and from the Jurassic and Cretaceous Predentates we learn that it has no tendency to turn backwards; it is an organ that has been deprived of its function by a bipedal mode of progression, it is fast dwindling, and in the case of *Iguanodon* only a stump of metatarsal remains.

In order to render the dissimilarity the more apparent, I have, in fig. 115, drawn the foot of *Anomæpus* from a plastic model, in order to compare it with the foot of *Archaeopteryx*. This makes it plain that the shank of the Trias-Predentates has had a position different from that of the birds, for the tip of the ungual of the first toe cannot reach the ground, unless the metatarsal slope considerably backwards so as to form an angle of about 42° with the ground. For this reason alone, the character of the foot becomes totally dissimilar to that of *Archaeopteryx*. The greatly shortened first metatarsal, moreover, is proof that the first toe would not, as the hallux of birds, be capable of grasping a branch; it is too far above the other toes for that.

From this we must infer that the Predentates have always moved about on the ground, and that never in their existence has there been any arboreal period, such as we generally ascribe to birds.

Another important difference is that the first metatarsal in *Anomæpus*, as also in the other Predentates, is shortened from the distal end, so that only the proximal half remains; while in the case of birds, on the contrary, it is the distal part that remains. The same thing holds good respecting certain Theropoda and Coelurosaurs, and in that way we get an idea of the evolutionary process through which the hallux of the birds has passed in order to attain the form which we find already in the Jurassic birds.

The foot of *Antrodemus* (fig. 115, 6) shows us the first stage, the first metatarsal being in process of reduction, so that the middle portion of the shaft

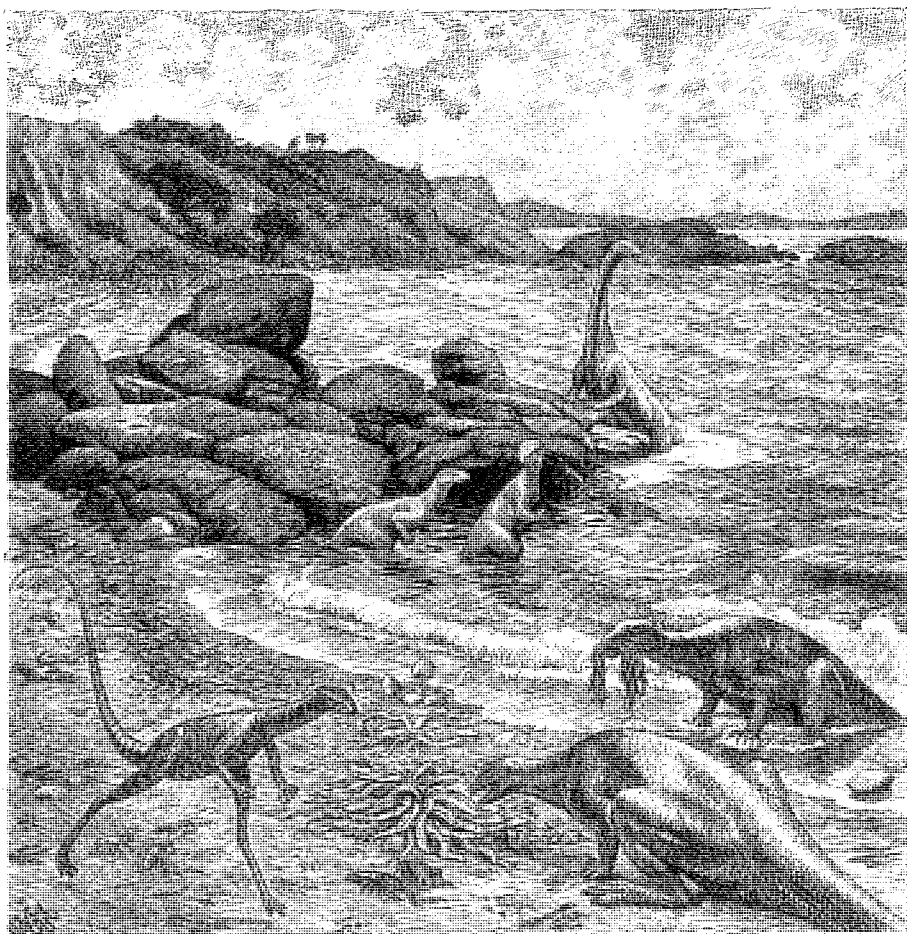


Fig. 114. Triassic life on the shore of a lake. In the foreground the swift running *Podokesaurus holyokensis* and two Predentates of the *Anomæpus* or *Sauropus* type. In the middle two small *Nanosaurus*-like Predentates.

is entirely wanting. Next disappears the proximal part of this metatarsal as we see it in *Ceratosaurus* (fig. 115, 7), and the result is the hind-toe characteristic to birds, with its metatarsals reduced to the distal portion and loosely attached to the inner and hinder surface of the other three coalesced metatarsals.

The hallux of the Predentates does not show the slightest trace of such an evolution; its reduction takes the opposite course, hence it could not possibly become the hind-toe of the birds.

O. Abel (2) has furnished us with the drawing of a foot of *Hypsilophodon foxi* (fig. 115, 1), about which he says that it is "a forcipated foot for grasping and climbing" (einen Zangenfuss zum Greifklettern), which the animal must have used "like an arboreal bird" (wie ein Baumvogel), because it led an

arboreal life. He tries to prove this by pointing out that the toes of the fossil are bent backwards and might be opposable to the hallux. It does not seem to me that this can be cited in proof, for the foot of *Procompsognathus triassicus* (16), for instance, displays a still stronger bend of the toes, and yet no one would on that account designate this marked cursorial type "aboreal".

Moreover, Abel says that his drawing is a combination of several individuals from the collection in the British Museum, "mainly on the basis of the original by Hulke". Hulke's drawing of this foot (20) seems to be a very accurate reproduction of the fossil, and it does not at all look like Abels's drawing.

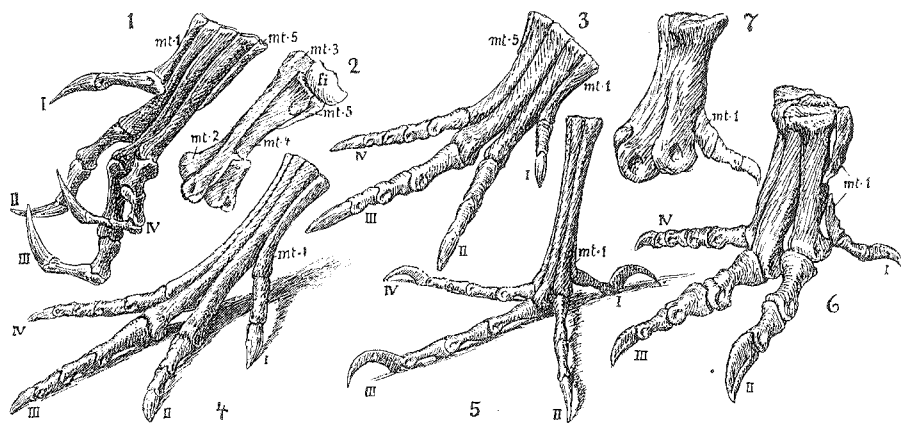


Fig. 115. 1—3 Right foot of *Hypsilophodon foxi*, 1 from a drawing by O. Abel, 2 metatarsals after J. W. Hulke, 3 reconstructed after the fossils reproduced by J. W. Hulke, 4—6 right foot of 4 *Anomæpus* (see fig. 112 C₂), 5 *Archaeopteryx*, 6 *Antrodemus valens* after Gilmore, 7 metatarsals and first toe of *Ceratosaurs* after Gilmore.

The phalanges of the fourth toe are contiguous and fully stretched out, as I have reproduced them in fig. 115, 3. They show the usual shortening peculiar to this toe, while in the drawing by Abel we see some thin and slender phalanges in the fourth toe. Besides, Hulke has furnished us with exact measures of all visible particulars; Abel's drawing does not correspond to these, either, and the first phalanx of the first toe, for instance, is twice as long as indicated by Hulke. In my opinion, moreover, if Abel's drawing were correct, it would not be possible for the animal to move its first toe without collision of same with the second metatarsal.

The exact position of the first metatarsal cannot be made out from the fossil, but on the analogy of the other Predentates, it must have come very close to my drawing in fig. 115, 3. The foot of *Hypsilophodon* appears to have been much like that of *Anomæpus*, only the metatarsals are shorter. I cannot agree with O. Abel that *Hypsilophodon* was arboreal. The displacement in proximal direction of the hallux would also render it impossible for the animal to grasp a branch "like an arboreal bird"; in order to grip the branch at all, the first metatarsal would have to be mobile, as the first

metacarpal of the human hand. But Hulke writes that the proximal ends of the metatarsals "are in closest mutual apposition".

The hand of *Hypsilophodon* (fig. 116, 5), moreover, does not look as if it were specialized for climbing. The pelvis of the animal is of the same character as that of *Stegosaurus*, and hence, according to Dollo, it should be quadrupedal. Nopsca (21) also says that its "dermal armour is a character in which *Hypsilophodon* approaches more closely the armour-clad *Stegosaurus*

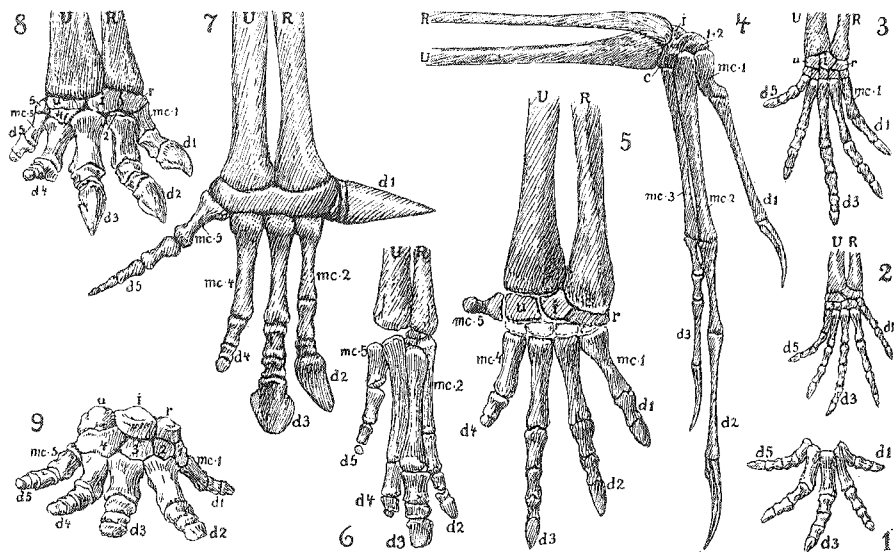


Fig. 116. Right hand, dorsal view of 1 *Otozoum moodii* (see fig. 113 B), 2 *Sauropus barrattii* (fig. 113 D), 3 *Anomæpus scambus* (see fig. 112 B), 4 *Archaeornis*, 5 *Hypsilophodon foxi* after J. W. Hulke, 6 *Trachodon* after Barnum Brown, 7 *Iguanodon* after Dollo, 8 *Camptosaurus dispar* after Gilmore, 9 *Coryphodon testis*, an amblypod mammal from the Lower Eocene, after Osborn, lettering as before.

and *Ceratopsia*, than any other Orthopodous Dinosaurs". Arboreal types, as a rule, do not seem to be equipped with dermal armour.

The shoulder-girdle of the Predentates have no clavicles, and this in itself is sufficient to render the derivation of the birds from these animals an impossibility. It still remains for us to compare their hand with that of *Archaeornis* (fig. 116). I am unable to see any real resemblance between them. Fig. 19 showed a marked tendency in Theropoda and Coelurosaurs toward a reduction of digits from the ulnare side, and a lengthening of the second one, just as in *Archaeornis*. The specializing of the hand in the Predentates, on the contrary, leaves a strange and confused impression. There is no pronounced tendency in any direction; each species seems to have undergone its own special transformation of the hand. *Iguanodon* has a very elongated fifth digit, and a highly specialized first one, while in *Hypsilophodon* the first is normal and the fifth vestigial. The hand of *Camptosaurus* resembles that of

a heavy quadrupedal mammal (fig. 116, 8 and 9), and Gilmore (12) says about the eight carpals: "The proximal row forms two distinct concave surfaces for articulation with the distal ends of the radius and ulna. These articulating surfaces are clearly defined, as in many of the fore-limbs of the mammalia". In the hand of *Trachodon* we have still another type, the first digit being absent. The fifth metacarpal is very short and divergent; the other three are closely appressed throughout the whole length (22). As in the other Predentates, the proximal row of the phalanges is the longest, and the penultimate phalanges, especially in *Iguanodon* and *Trachodon*, are quite small and irregular. The very reverse is the case in *Archaeornis*, whose penultimate phalanges are very elongate and finely shaped. The Stegosaur has an altogether elephant-like hand.

From the footprints I have reconstructed the primitive hands of three Trias-Predentates (fig. 116, 1—3), and, however improbable, it is of course not wholly impossible for a hand of *Anomæpus*, for instance, to change into that of *Archaeornis*. But the second digit is not the longest, and we see from the later Predentates that the tendency to reduction of the digits is quite another than in *Archaeornis*.

We have now compared the chief parts of the skeleton of the Predentates with those of the Jurassic birds, and have hardly found any points of resemblance between them. The transformation of the cranium diverged from bird-like characters, and even the sclerotic ring was quite unlike that of a bird. The teeth were so dissimilar as they possibly could be. Highly significant, too, was the absence of ventral ribs, and of clavicles. Ilium and ischium were not like those of *Archaeopteryx*, and of the anterior, very prominent part of the pubis, nothing corresponding was found in the pelvis of *Archaeopteryx*. In the Predentates, the fourth trochanter of the femur was far more developed than in birds, and its presence could not very well play any important part by way of evidence, inasmuch as the Theropodous Dinosaurs and the Coelurosaurs had a well developed fourth trochanter. As far as the foot was concerned, the position and the direction of the hallux, particularly, were conclusive. The most bird-like feature was the shape of the tarsals, the joint being in the middle of the tarsus as in birds. And yet, the ascending process from the intermedium was wanting, thus marking, also in the tarsus, an important distinction between Predentates and birds. Neither did the hand show any likeness to that of *Archaeornis*. All in all, the evolutionary process of the Predentates must be said to be tending away from likeness to birds.

I do not think, therefore, that Professor Lankester will derive any satisfaction from letting his *Iguanodon*-stock beat the air with its paddle-like front limbs. Statements of that kind, based on a wholly superficial comparison of a few particulars, but deficient in any real evidence, are not advancing to science, and ought never to find expression.

Not only are the Predentates very dissimilar to birds; also with the Theropoda and Coelurosaurs they offer vital points of disparity, and hence I fully agree with O. Abel (10), who distinguishes them from the Dinosaurs

as an entirely different order. F. v. Huene, too, the eminent Dinosaur-connoisseur, had already in 1914 ("Saurischia and Ornithischia", Geological Magazine) come to the conclusion that the "Dinosauria are not of monophyletic origin, and should therefore be considered as two distinct natural orders".

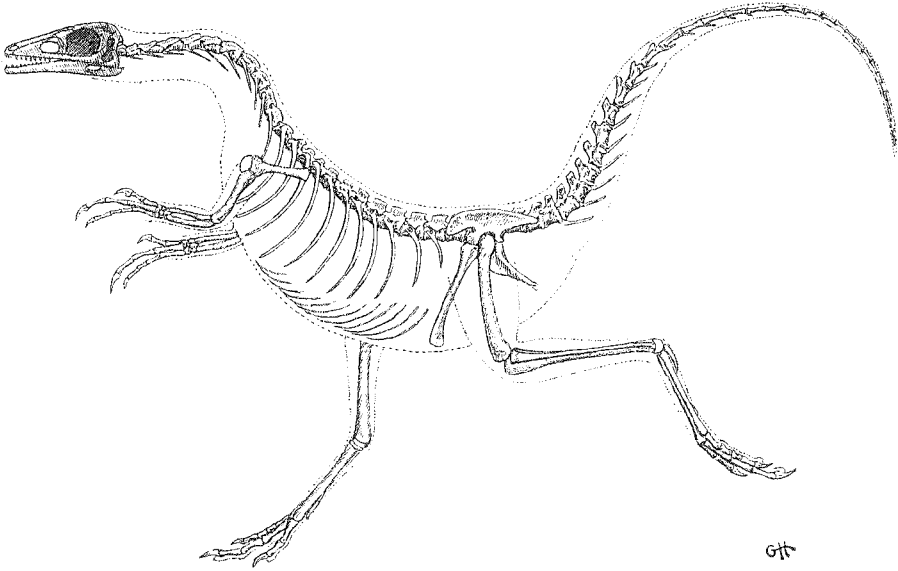


Fig. 117. Skeleton of *Compsognathus longipes* from the Upper Jurassic of Solenhofen, restored by the author from a photograph of the fossil (F. v. Huene).

COELUROSAURS

On turning from the clumsy Predentates to the Coelurosaurs, we meet with quite a different type; the very name of one of these, *Podokesaurus*, e. i. the light-footed saurian (fig. 114) is suggestive of the whole group. Hollow bones of very light structure, exceedingly long hind-limbs with strongly elongate metatarsals and a "hind-toe", a long, narrow hand, a long tail and a long neck, large orbits and ventral ribs — these are bird-features immediately conspicuous.

We encounter the "fine-jawed" *Compsognathus longipes* (figs. 117 and 119) from the Upper Jurassic, with its long feet, and its supposed forerunner, *Procompsognathus triassicus*; *Saltopus*, i. e. the jumper; *Coelurus*, the hollow-tail; *Ornitholestes*, the bird-robber, and *Struthiomimus*, the Ostrich-mimic, which, presumably, has progressed with the speed and lightness of an ostrich across the plains of the desert. It might thus be possible to find the ancestor of birds amongst these bipedal Coelurosaurs, but they are all wanting a pelvis "quite suggestive of that of a bird".

To make comparisons more complete we shall, in this section, also refer to some of the Theropodous Dinosaur, e. g. *Anchisaurus*, *Antrodemus valens*, *Ceratosaurus*, *Tyrannosaurus*, and *Gorgosaurus*.

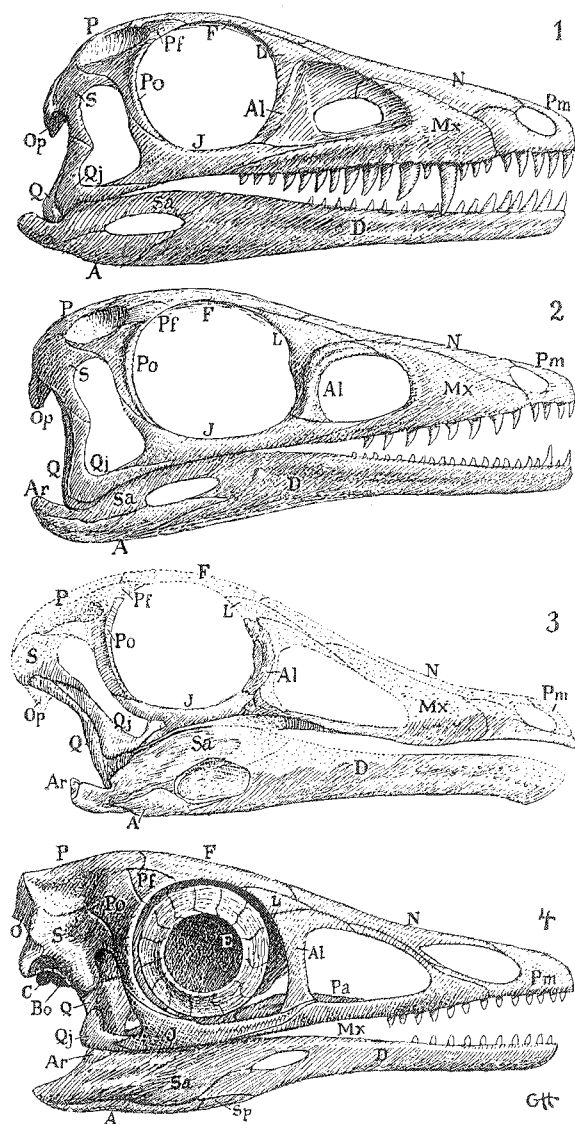


Fig. 118. Skulls in side view of 1 *Procompsognathus triassicus* from the Keuper of Germany after F. v. Huene, 2 *Compsognathus longipes* from the Upper Jurassic, restoration by the author, 3 *Struthiomimus altus* from the Upper Cretaceous of Alberta after H. F. Osborn, 4 *Archaeornis siemensi* by the author, lettering as in figs. 3 and 5.

Fig. 118 shows the skulls of three Coelurosaurs from the Triassic, the Jurassic, and the Cretaceous respectively, compared with that of *Archaeornis*. The small changes taking place throughout millions of years are tending towards a bird-like, light, and delicate bony structure. The teeth, lodged in distinct sockets, also have the same character as those of *Archaeornis*, and there is a tendency to a reduction in size of the teeth, ending in toothlessness as in birds. About *Struthiomimus*, Osborn (23) says as follows: "The unique feature of the skull is the total absence of teeth and indications that the premaxillaries and dentaries were sheathed in narrow horny beaks somewhat similar to those of *Struthio*".

He further speaks about "the great size of the orbit, which is relatively as large as in *Struthio*". "The anterior inclination of the lower end of the quadrate" is also present in *Archaeornis*, but not "the vertical elongation of the quadrate-quadrato-jugal".

When otherwise comparing the position and form of the individual bones, we are struck with their likeness to those of *Archaeornis*. Premaxillary is identical, the long nasal, maxillary, frontal, etc., practically so, only that the distance between the narial opening and the preorbital fenestra is larger in the Coelurosaurs than in *Archaeornis*. But posteriorly the jugal broadens considerably as in the latter; the mandible, too, is very similar.

The preorbital fenestra seems to be on the increase in the course of time, and the adlachrymal is of a peculiar shape in these Coelurosaurs.

The only real difference is due to the enlargement of the braincase in *Archaeornis*, and the connection between the squamosal and quadratojugal discontinued in birds.

Already in Part I we called attention to the fact that the occipital condyle in *Compsognathus* was composed of elements from both the exoccipitals and the basioccipital as it is in young birds (fig. 31). The same thing holds true of Theropodous Dinosaurs, e. g. *Antrodemus* (14). In top view the skull of

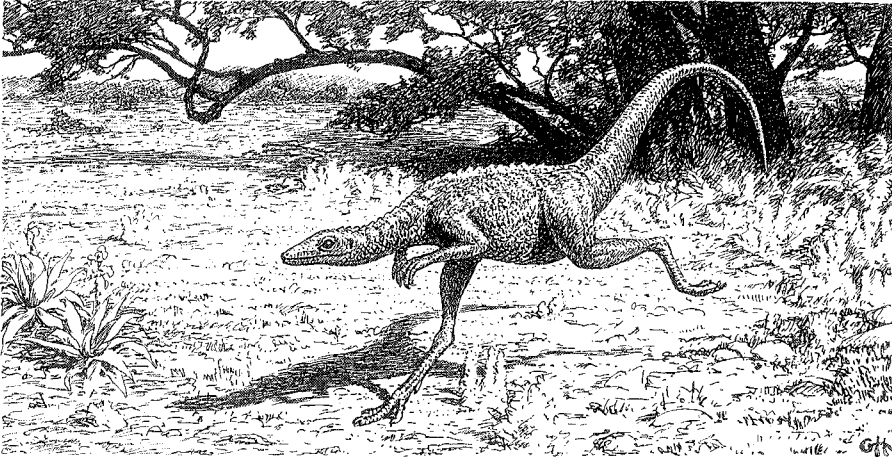


Fig. 119. Restoration of *Compsognathus longipes* by the author.

Procompsognathus (16) comes very close to that of *Euparkeria*, which in fig. 6 is compared with that of *Archaeornis*.

To furnish the reader with an idea of the outward appearance of these light and swift animals, I have in fig. 119 drawn the restoration of a typical Coelurosaur, the small *Compsognathus longipes*, with the bulk of a domestic cat.

A comparison between vertebræ is impossible, because those of *Archaeornis* are in a bad state of preservation. But in fig. 120 we may compare the neck vertebræ of *Hesperornis* with those of *Struthiomimus*. Osborn (23) says about these: "The cervical centra are uniformly elongate and the cervical ribs, instead of being loosely attached as in *Ornitholestes* and in the typical Theropoda, are abbreviated and closely coalesced to the sides of the centrum and neural arch". Exactly the same thing may be said about the cervicals of *Hesperornis*, and the resemblance to those of *Struthiomimus* is very close. Osborn states that the form of the centra "is an indication of a long, flexible, and powerful neck, as in *Struthio*".

The centra of the vertebræ in the primitive birds have slightly concave anterior and posterior articular surfaces, and this is seen in many of the Theropoda as well. Ventral ribs are also present in the Coelurosaurs; fig. 7, 2 shows those of a Theropodous Dinosaur.

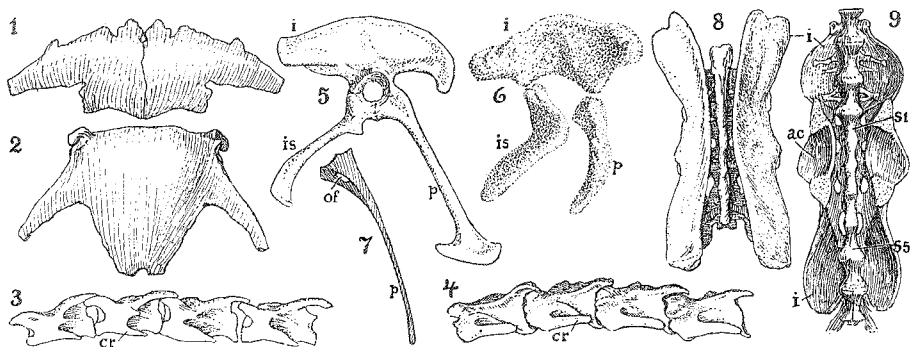


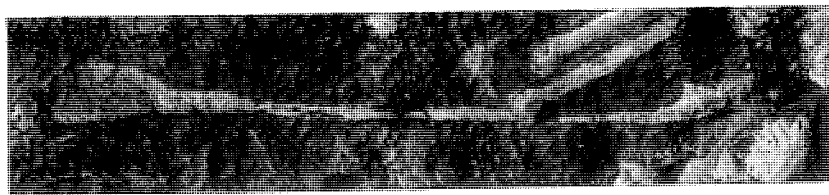
Fig. 120. 1 and 2 sternum of 1 *Gorgosaurus libratus* from the Cretaceous of Alberta after L. W. Lambe, 2 *Pachyornis elephantopus* from the Pliocene after Lydekker; 3—4 cervical vertebræ of 3 *Struthiomimus* from the Cretaceous after Osborn, 4 *Hesperornis* from the Cretaceous after Marsh; 5 pelvis in side view of *Struthiomimus* after Osborn, 6 embryonic pelvis of Blackheaded gull (*Larus ridibundus*) after Lebedinsky, 7 pubis of *Procompsognathus triassicus* after F. v. Huene, 8 the sacro-iliac arcade, superior view of *Tyrannosaurus* from the Cretaceous after Osborn, 9 sacrum and ilium, ventral view, of *Ceratosaurus* from the Upper Jurassic after Gilmore; ac acetabulum, cr cervical ribs, i ilium, is ischium, p pubis, S₁ and S₅ first and fifth sacral vertebræ.

Not knowing the sternum of the Jurassic birds (34), we must confine ourselves to a comparison of breastbones, as shown in fig. 120. Both of them, it is true, belong to degenerate types, the fore-limbs of *Gorgosaurus* (25) dwindling fast (fig. 124, III), as also is the case of *Dinornis*, but they go to prove that even in the reduction of skeletal elements reptiles and birds pursue the same course.

We learned in Part II that in the embryo of birds the pelvis was composed of the same elements as in reptiles, arranged in the same form of three rays; the pubis at first pointing forward and downward (fig. 73, 1—3 and fig. 120, 6) as in the preformation of the reptilian pelvis (fig. 73, E). While the pubis of the reptile retains its forward directed position (fig. 120, 5), it turns more and more backward in the bird-embryo, but from this it is evident that the pelvis in birds and in reptiles has the same origin.

As a matter of fact there is thus far greater likeness between the pelvis of bird and that of Coelurosaur than between those of bird and Predentate, which latter has a pubis directed both forward and backward, so infatuating to many scientists. And when looking at the isolated pubis of a Coelurosaur

Fig. 121. Pubis of *Podokesaurus holyokensis* from the Connecticut Trias from a photograph kindly forwarded by R. S. Lull.



from the Triassic, long and slender in form (fig. 121), we are forcibly reminded of the pubis in the Jurassic birds. It has even the same dilatation of the distal end as in *Archaeornis* (fig. 9, III). That also an obturator foramen has been present in the pubis proper, just as in *Archaeopteryx*, will appear from fig. 120, 7, which represents the pubis of *Procompsognathus triassicus*.

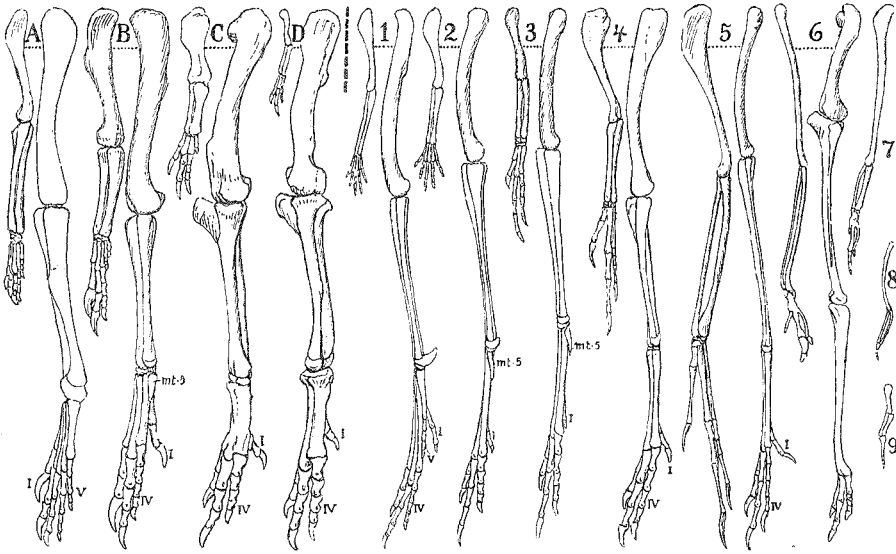


Fig. 122. Proportions of fore- and hind-limbs, these last reduced to the same length so as to show the diminution of the fore-limb in the Theropodous Dinosaurs and in birds, and the increase of same in the Coelurosaurs. A and 1 Pseudosuchians, B—D Theropodous Dinosaurs, 2—4 Coelurosaurs, 5—9 Birds; A *Ornithosuchus woodwardi*, B *Anchisaurus colurus* after Marsh, C *Ceratosaurus nasicornis* after Gilmore, D *Tyrannosaurus rex*. 1 *Saltoposuchus longipes*, 2 *Procompsognathus triassicus*, 3 *Compsognathus longipes*, 4 *Ornitholestes*, 5 *Archaeornis*, 6 *Rhea*, 7 *Ostrich*, 8 *Kiwi*, 9 *Emeu*. A from the Middle, B, 1 and 2 from the Upper Triassic, C, 3, 4 and 5 from the Upper Jurassic, D from the Upper Cretaceous; A, 1 and 2 after F. v. Huene, D and 4 after Osborn.

In the process of time, the distal end of pubis, both in Coelurosaurs and Theropodous Dinosaurs, has developed a remarkable, triangular, foot-like expansion (fig. 120, 5 and fig. 107, 1). The weight of the body was, presumably, partly supported by this pubic "foot" whenever the animal assumed a squatting position.

There was an increase in the number of coössified vertebræ in the sacrum, from three to five, and a lengthening of the ilium. We quote again from Osborn (23) about *Struthiomimus*: "Superiorly the sacral spines unite in a continuous single, closely compressed plate, wedged in between the iliac borders". From fig. 120, 8 we see that the same was the case in *Tyrannosaurus*. Also in ventral view does the pelvis of a Theropodous Dinosaur present a strikingly bird-like appearance, there being a strong tendency to incorporate both the lumbar and caudal vertebræ in the sacrum (fig. 120, 9).

A remarkable difference seems to exist between the fore-limbs of The-

ropoda and those of Coelurosaurs. It is a well-known fact that a Theropodous Dinosaur from the Trias has a much longer arm and a more primitive hand than one from the Jurassic, and that the fore-limb of a Theropodous Dinosaur from the Cretaceous has undergone a still further reduction. But nowhere have I found a statement to the effect that any lengthening of the fore-limbs seems to take place in Coelurosaurs.

In fig. 122 I have reduced the hind-limbs to the same lengths, and we are thus enabled to compare the fore-limbs directly. The illustrations speak for themselves. B—D are Theropous Dinosaurs, 2—4 Coelurosaurs, and if we glance from the fore-limb of *Ornitholestes* to that of *Archaeornis*, an intermediate transitional form suggests itself.

In our reference to the hand (fig. 19) we have already thoroughly discussed the reduction of the digits in number and size, from the ulnar side. We also pointed out that the specialization of the hand developed along the same lines in Coelurosaurs and in birds; the shortened first metacarpal, the long second digit, the elongation of the penultimate phalanges and the shortening of the two proximal phalanges of the third digit being in this respect very remarkable. There was likewise a lateral compression of the manus in both, and we arrived at the conclusion that the tridactyl hand of *Ornitholestes* bears the most striking resemblance to that of *Archaeornis*.

If we start from the very primitive hand of *Procompsognathus triassicus* (see also fig. 124, I) and through a *Compsognathus*-like hand pass on to that of *Ornitholestes*, we have before us the whole evolution of this unique tridactyl hand of the birds.

Although the materials for comparison are inadequate, it is possible, by reference to figs. 122 and 124, also in the degeneration of the fore-limbs owing to disuse, to see points of similarity between Dinosaurs and birds. It is the normal process for all classes, I suppose, that the distal parts are the first to vanish, and yet, deviations from the rule might be conceived. In Sirenia and Whales the hind-limb is so degenerate that, as a rule, a vestigial femur only remains of the limb. Hence, we cannot decide in what way the dwindling of the limb commenced in their cases, but in the hands of not a few mammals the first digit is the first to disappear.

In many modern lizards whose bodies have grown more snake-like, the limbs are also about vanishing. The reduction commences with the disappearance of the ultimate phalanges of the digits (24). It nearly always starts with the fifth digit, then the fourth, and so on. The metacarpals vanish from the ulnar side as well. This seems, then, to be the normal process of reduction both in fossil and recent reptiles.

In Rhea (fig. 122, 6) all the detail of the skeleton of the bird's wing is still intact, but as a whole the hand has shortened considerably; in the Ostrich, too, the forearm is shortened, in the Kiwi there is a further shortening of the hand and the loss of two digits, the third and the first. This is also the case in the Emeu, whose humerus is greatly shortened as well, and whose fore-limb is dwarfish in proportion to the hind-limb.

It is possible that future finds will show us a bird with two digits of the hand left, but the Belly River formation of Alberta has supplied a complete skeleton of a Dinosaur, *Gorgosaurus libratus*, whose hand has only two digits, the third metacarpal being vestigial (fig. 124, III).

Gorgosaurus, as described by L. W. Lambe (25) was of great size, the full



Fig. 123. Gorgosaurs at the carcass of a Stegosaur, late afternoon idyl from the Cretaceous, drawing by the author.

length about 29 feet; "it was lightly built and had long bird-like hind limbs on which the moderately slender, lizard-shaped body, tapering to the narrow head and into the long tail, was balanced when the creature stood or walked". The animal moved on its strong hind-limbs only, the fore ones being extremely short and relatively feeble. Lambe believes that *Gorgosaurus* was sluggish and not a quick mover, and that it fed mainly on carcasses, the minute fore-limbs being of no use in securing prey. Its perfect teeth, showing no abrasion, suggest a soft food, for which reason *Gorgosaurus* was not considered an intrepid hunter, but a scavenger, somewhat in the same manner as the modern Hyena, — some rather formidable Hyenas, however, it must have been (fig. 123).

And yet it is strange that this animal almost wholly has stopped using its fore-limb. The next step we observe in the wing of Cassowary (fig. 124, IV), where only one digit is left, and the three metacarpals have fused completely together, the first and the third seen only as small prominences at the proximal part of the second one. In the embryo of the Kiwi, which also has but the

second digit left, we see the first and third metacarpals distinctly separate from the second (fig. 124, VII).

As the proximal elements of course are the most conservative, I have reduced the fore-limbs, shown in fig. 124, to the same size of the scapula for the sake of better comparison. The whole hand also being lost, we arrive

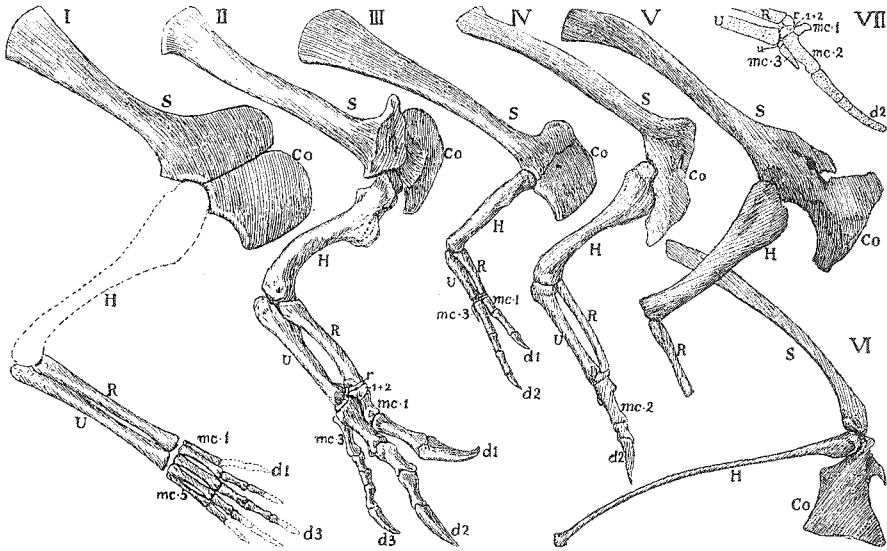


Fig. 124. Right shoulder-girdles and fore-limbs of reptiles and birds reduced to the same length of the scapula so as to show the shortening of the arm and the reductive specialization of the hand. I *Procompsognathus triassicus* after F. v. Huene, II *Antrodemus valens* from the Upper Jurassic after Gilmore, III *Gorgosaurus libratus* from the Cretaceous after L. W. Lambe, IV Cassowary, V *Diatryma steini* from the Eower Eocene after W. D. Matthew and W. Granger, VI *Hesperornis regalis* from the Cretaceous after Marsh, VII hand of embryo of Kiwi after T. J. Parker. Lettering as before.

at the vestige of a fore-limb such as the bizarre *Diatryma steini* (fig. 124, V) kept concealed under its long, hair-like feathers; — of the forearm only the radius is left. Finally, in *Hesperornis* (VI) the last remnant of the entire fore-limb is the humerus, a long bone, thin and feeble, of no use at all to the bird.

In scapula and coracoid there are also considerable resemblances. Gilmore (14) says: "The scapula of *Antrodemus* is distinctive on account of its bird-like form". The degenerate coracoid of the birds nearly assume reptilian shape once more, and the angle it forms with the scapula becomes more obtuse. Speaking of *Diatryma*, Matthew and Granger (26) say as follows: "The coracoid and scapula are solidly fused together, meeting end-on as in the ratite birds instead of at a sharp angle as in carinate birds".

This curious bird (fig. 125) "lived during the Lower Eocene, near to the beginning of the Age of Mammals, and was contemporary and associate of the little *Eohippus* or Fourtoed Horse" (26). "In bulk of body and limbs it equalled all but the largest of the moas and surpassed any living bird, but

was not so tall as an ostrich. The height of the reconstructed skeleton is nearly seven feet. The neck and head were totally unlike any living bird, the neck short and very massive, the head of enormous size with a huge compressed beak". In all probability it lived on small reptiles and mammals, which it could easily overtake, and kill at a blow with its heavy beak.

Having now seen what the primitive hand with its five well developed digits has become during the evolution of the Dinosaurs in the process of millions of years, we naturally meet with the query: Why should it degenerate, why could it not evolve into something like the human hand? By the bipedal mode of progression, the hand was no more needed as a support to the forepart of the body in walking, and the erect position of the animal as also the grasping power of the hand would, we should infer, be propitious to further development of the digits by way of mobility and opposability. But the very reverse takes place; one after another the digits are lost.

In all probability the answer to this question would be as follows: No, this could not be done, because the brain of these reptiles was very small and undeveloped. Not till the Miocene or Pliocene, when in the precursors of man the development of brain commenced, was it possible for hand and brain to react upon and stimulate each other.

I cannot consider this as any real solution, however, for it is nothing but a paraphrase of well-known facts in the form of replication. We do not learn why the reptilian brain did not begin to develop in the Triassic, although we have seen in the case of both Pterosaurs and birds that it possessed special capabilities for development.

If then it be urged that a warm-blooded organism was requisite to the development of the brain, we are once more at a loss to understand the argument, inasmuch as mammals existed already in the Triassic; nevertheless, as late as the Eocene the archaic mammals were greatly limited in their potential mentality, having but very small brains. Not till the close of the Eocene were they superseded by the modernized forms with a brain power capable of further development.

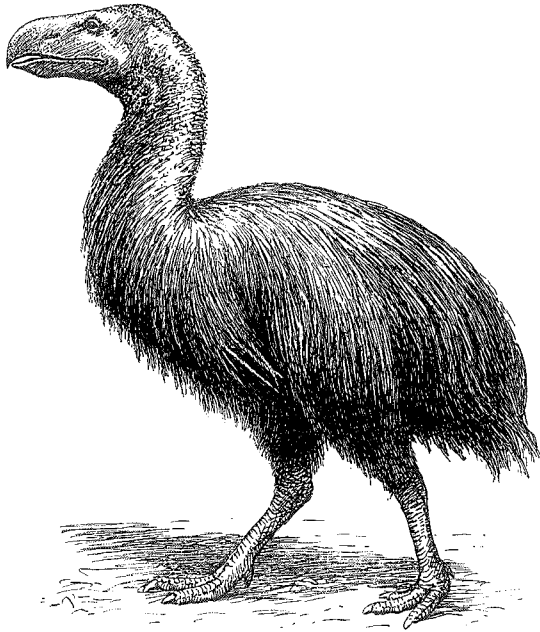


Fig. 125. Restoration of *Diatryma steini* from the Lower Eocene after W. D. Matthew and W. Granger.

We really do not know what has been the moving power in the special development of the brain. We see how climate and environment in the course of time have reacted, in a most remarkable way, upon the various animals; an almost unlimited plasticity of the whole body enables it to adapt itself to the most different conditions of life: flying in the air, swimming in and on the water, wading through fens and moors, digging under the ground, climbing the tops of trees, or running across steppes. The mode of progression results in a transformation of the limbs, and the difference of food changes the teeth. The fossil skeletons very plainly show that these changes have taken place, and which forms they have assumed within the various orders. That the inner organs have kept pace with these transformations, must be taken for granted, although it has been possible to verify it in exceptional cases only. We actually know nothing of either shape or size of the brain itself but what we can infer from the castings of the braincase cavity.

The brain enters into contact with the surrounding world through the organs of sense, and amongst these, optical impressions are of the first importance. The Coelurosaurs had a large orbit (fig. 118), and reptiles closely akin to them had a well developed sclerotic circle (fig. 5, B); we must conclude, therefore, that they possessed an excellent eye capable of conveying to the brain distinct optical images of the surroundings. The constant repetition of certain optical impressions will, by linking these together, produce some faculty of association, which is the precursor of intelligence. And for me it is not unreasonable to imagine that such rays of intelligence were dawning on the Coelurosaurs.

It is not conscious intelligence as such, however, that produces the various adaptations of the body to the surrounding conditions. We do not believe, as Lamarck did, that the animals have acquired their new organs simply by wishing for them, for of course no brain is capable of expressing a wish for the change of an organ the character and use of which is as yet unconceived.

Our nearest guess is that such a change is produced by certain surroundings reacting upon particular nerve centra in the subconscious life of the animal so as to release in the respective organs small changes, which in the course of time prove to be of great, perhaps radical, importance to the entire organism. But the whole process is carried on without communicating itself to the brain by way of consciousness as such.

A special transformation of the hand, however, took place in the later Coelurosaurs, after they had lost two of their digits. Osborn (23) writes: "The phalanges of the pollex are divergent and rotated inwards in the two genera *Ornitholestes* and *Struthiomimus*" (fig. 19, III and VI), and W. K. Gregory (23) says of *Struthiomimus*: "By virtue of the twisting of the first metacarpal the phalanges of the first digit could be turned partly toward the other digits so that the manus was to a certain extent prehensile". And the tridactyl hand of birds was developed in such a manner that it gave rise to their world-wide dispersion, thus furnishing special stimuli to the development of their brain.

And further, *Struthiomimus* has dispensed with its teeth, a result not yet attained by man, but evidently in view.

After this little digression we shall return to our comparison of Coelurosaurs and birds. — The femur with its well developed fourth trochanter has already been mentioned (fig. 109, 3 and 4), the tibia and fibula are exactly like those of the Jurassic birds, and the tarsus with its ascending, bird-like,

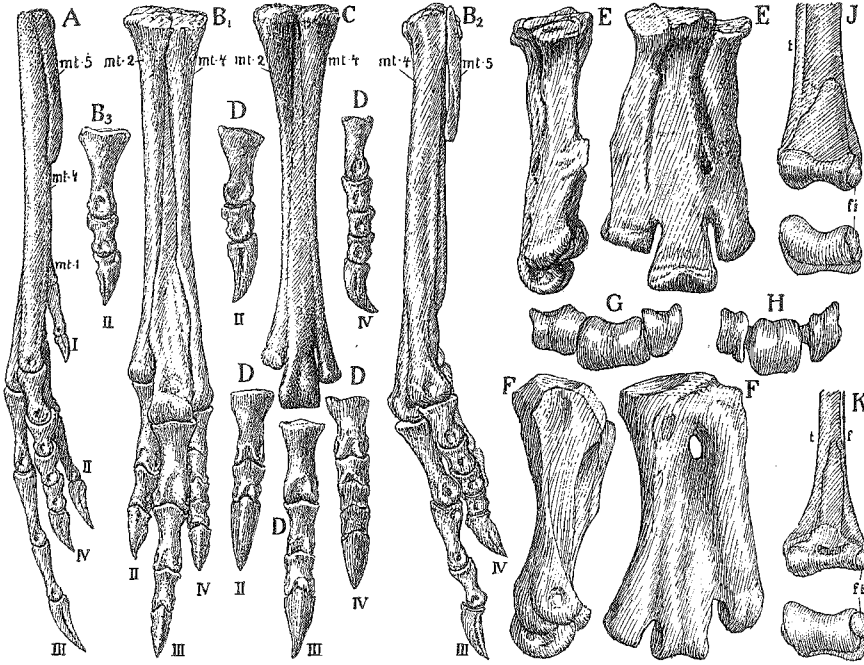


Fig. 126. Left foot of A *Procompsognathus triassicus* drawn from the fossils reproduced by F. v. Huene, B₁₋₃ *Struthiomimus altus* from the Cretaceous after Osborn, B₁ anterior, B₂ external view B₃ second toe, internal view; left metatarsals of Chick (*Gallus dom.*) anterior view, D toes from the left foot of *Dinornis parvus* from the Pleistocene of New Zealand after Owen, anterior internal and external views; E and F left metatarsals of E *Ceratosaurus nasicornis* from the Upper Jurassic after Gilmore, F *Perispheniscus winani* from the Eocene of Seymour island after Ameghino, G and H inferior view of metatarsals of G *Ceratosaurus* after Gilmore, H Cassowary after Owen; J and K distal part of the tibio-tarsus, anterior and inferior views of J *Ornithomimus velox* from the Cretaceous, K Ostrich, both after Marsh.

intermedium was shown in fig. 109, C. For a further comparison we refer to fig. 126, J and K.

This figure also presents the highly interesting metatarsals and toes of Coelurosaurs together with those of birds. The resemblance is so close that we should take them to be two species within the same genus, and not the representatives of two different classes. It is almost impossible to imagine that B in fig. 126 really is the foot of a reptile, and not that of a bird. Osborn's description of the metatarsals might apply to those of birds (23): "The tarso-metatarsus consists of three closely coalesced median digits in which mt. 3 is thrust backward at the proximal end so that it only appears on the posterior face, while it is thrust forward at the distal end so that it makes

up the greater part of the anterior face of the pes, in which the third digit is much the longest". And when we look at the whole character of the toes, their shortened form, and the proportion between the number, shape, and size of the individual phalanges, every particular proves to be so exactly alike in reptile and bird as to be nothing short of amazing, the only real difference being that the vestigial fifth metatarsal persists in the reptile, but not in the bird.

The same tendency prevails in the Theropodous Dinosaurs. We quote from

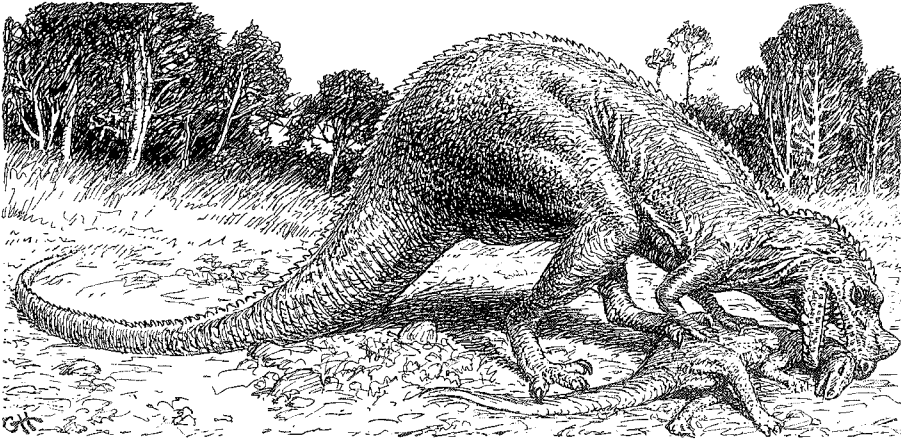


Fig. 127. *Ceratosaurus nasicornis* from the Upper Jurassic, completing the kill of *Camptosaurus nanus*, a small herbivorous contemporary, drawn by the author, making use of a model restoration by Charles W. Gilmore, 1915.

Gilmore (14): "The rather loosely articulated metatarsals of *Anchisaurus* and *Plateosaurus* of the Triassic progressively become more and more compactly united, thus exhibiting a more powerful and less mobile arrangement of the metatarsals, which in this respect attains the highest degree of specialization in the Upper Cretaceous genera". A good example of the latter is *Gorgosaurus libratus*, to quote L. W. Lambe (25): "The second, third, and fourth metatarsals with their elongation, their very close contact, and their distal divergence, need only to be co-ossified where in juxtaposition to produce a bone remarkably similar to the tarsometatarsus of the majority of birds". Another specialization is seen in *Ceratosaurus* (fig. 127) whose metatarsals (fig. 126, E) are completely coëssified, resembling in this respect those of the Penguin (fig. 126, F). Even the intermetatarsal foramen is on the same side in both, but placed a little higher in the case of the Penguin.

Procompsognathus triassicus presents a more primitive arrangement (fig. 126, A). According to F. v. Huene (16) the three metatarsals are fitted closely against one another throughout their length, not diverging distally either. They are entirely straight and compressed laterally, but not coëssified, their distal end presenting powerful articulating surfaces and deep pits on the sides. The first metatarsal has a somewhat median position, so as to leave the pha-

lances the more free and mobile. In fig. 113, 6 we saw how the small specialized first metatarsal originated in birds; in *Procompsognathus* this specialization has already set in, only still more so than in the original bird foot (fig. 113, 5), the first toe being displaced in proximal direction.

Just as in the case of *Struthiomimus*, there is in *Procompsognathus* a marked shortening of the phalanges of the fourth toe. It is surprising to find already in the Triassic so pronounced a specialization not yet attained by the Jurassic birds. The foot of *Compsognathus* (fig. 15) is in this respect also



Fig. 128. Three Frilled Lizards (*Chlamydosaurus kingi*), and a *Grammatophora muricata* on the right, all at full speed. Drawn by the author making use of the small instantaneous photographs by Saville-Kent.

more primitive. The whole structure of the foot of the Coelurosaurs points to a strictly cursorial function.

As observed by Saville Kent, *Chlamydosaurus* and other recent lizards, whose hind-limbs are not at all specialized for a bipedal mode of progression, are able to raise their fore-limbs, balance the anterior part of the body with the tail, and run along rapidly upon the hind-limbs (fig. 128). We may then easily imagine how much faster was the speed of the running bipedal reptiles of the past.

Compsognathus and *Ornitholestes* were comparatively small Coelurosaurs, "running and walking on their hind-limbs with the long tail stretched out behind to balance the body. From what we know of their tracks it seems that they walked or ran with a narrow treadway, the footsteps almost in the middle line of progress. They did not hop like perching birds, nor did they waddle like most living reptiles" (W. D. Matthew, 27). R. S. Lull (18) refers to the footprints of the cursorial, carnivorous Dinosaurs in the Connecticut Trias and calls their manner of locomotion "a true walk or run with alternating steps, which without exception the bipedal tracks show, there being no instance of the record of a jumping form". They were "so truly bipedal

that the manus and tail never impress. The pes is tetradactyl but only exceptionally does the claw of the strong grasping hallux leave a mark. The claws are rather pointed and the whole foot is very bird-like" (fig. 129).

But this being the case, why cannot these footprints have been produced by birds? R. S. Lull (18, p. 470) gives an answer to this question, saying: "The generalized arrangement of the pads, which, with the exception of the distal articulation, are mesarthral, that is, they lie opposite the phalanges as in the human hand and not arthral with the pads opposite the joints, as in all lizards and the majority of carinate birds, characterizes the earlier dinosaurs. Finally in certain of the Limicolae, namely *Phalaropus hyperboreus* (Coues: Key to North American birds 1884 fig. 53 bis) in which the foot retains its cursorial character without having become specialized for perching, the pads are arranged as in dinosaurs". And O. Abel is of exactly the same opinion when saying (2, p. 270 and 404), quoting Lull almost verbatim, that the toe-pads of Dinosaurs lie opposite the phalanges, while those of birds, on the contrary, lie opposite the joints, with few exceptions, for instance *Ph. hyperboreus*.

Such an agreement between two eminent scientists should of course carry conviction, but surprised at the exceptional position of the Red-necked Phalarope in this respect, we refer to Coues and look at the fig. 53 bis mentioned by Lull. Here we find the foot of this bird represented in profile in such a way that the rounded flaps of skin at the side of the toes hang downwards. That a scientist of R. S. Lull's rank should have taken these to be toe-pads, we dare not of course surmise. But we are at a loss to understand where he has got his information; in the text Coues does not say anything about the toe-pads.

So sweeping a statement as to the toe-pads of birds, in contradistinction to those of Dinosaurs, ought to be illustrated by drawings, showing the position of these toe-pads, but neither Lull nor Abel furnishes us with an illustration of a single bird's foot, although any one could easily get hold of such an object.

It would take us too far from our subject to examine the toes of all birds, but those few that I have studied and drawn show that the position of the toe-pads in birds are far more heterogeneous than supposed by Lull and Abel. In fig. 130 a, we see a hypothetical section through the toe of a Dinosaur showing R. S. Lull's conjecture as to the position of its pads. These lie exactly as, according to fig. 131 A, we see it in a Rook, viz. one under each phalanx. In the Swan (B) the very opposite is the case, they lie under the joints; and in the Stork (C) there is a combination of both, a weak and but little prominent pad appearing under both phalanx and joint. In the Pigeon (D) again it is different, there being two pads under each phalanx, but in a single place there is also one under a joint. Besides, we meet with individual differences, and it would be necessary to have a pile of material at one's disposal in order to say anything definite about it. The misjudged Red-necked Phalarope (G) has its pads just under the joints, and so has the Grey Phalarope (longitudinal section F).

Considering how different may be the position of the pads in birds, we begin to doubt that their regularity in the case of the Dinosaurs has been so great as supposed by Lull, that is to say, always opposite the phalanges. I particularly wish to call attention to the bird-like footprints, called *Grallator*, of which Lull (15, p. 200) says that they have "distinct phalangeal pads". The *Grallators* are "characterized by very long limbs and small, compact feet without an impressing hallux and with no tail trace. The proportions of length of

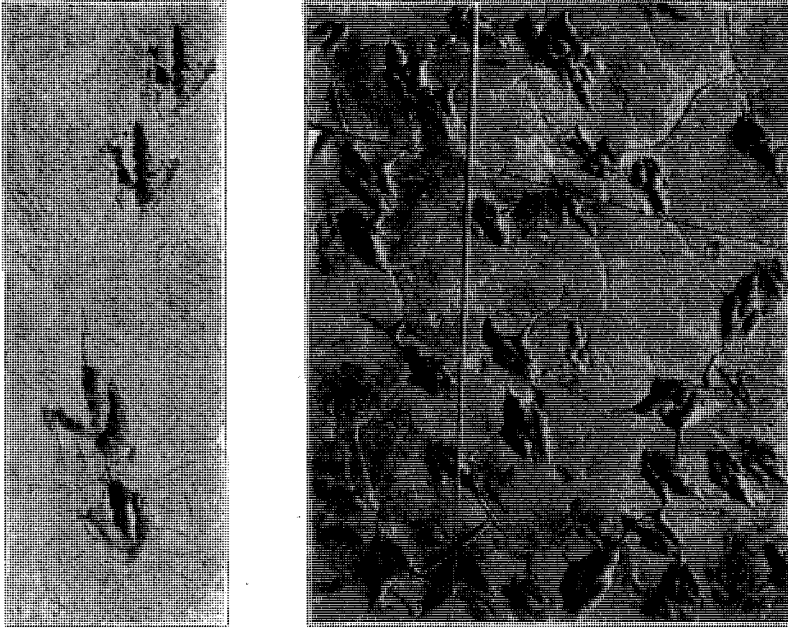


Fig. 129. Tracks of Cassowary in soft clay (to the left) and fossil Dinosaur tracks from the Triassic of Connecticut (R. S. Lull), after C. W. Beebe.

limbs to those of feet are the same as in the bustards, and the forms which made the tracks were probably aberrant carnivorous of habits, somewhat similar to those of wading birds, possibly feeding upon feebler reptiles and amphibians, or on fish" (18). "*Grallator* comprises, for the most part, small forms, the smallest species, *G. gracilis* (fig. 130, i), indicating a creature but two thirds the size of *Compsognathus*, the smallest known dinosaur" (18).

About *Grallator cursorius* (fig. 130, h) Lull says (15) that it "corresponds with the compsognathoid dinosaur *Podokesaurus holyokensis* Talbot in form and proportions, horizon and locality". The metatarsals of this small Dinosaur "are so closely appressed together as to form a wonderfully compact structure" (15, p. 168), and it therefore seems impossible for the widely separated proximal ends of the three digits he has drawn in the track to articulate with this "compact structure". Moreover, it is only a part of phalanx 1 of the fourth toe that is drawn, so the distance between the proximal ends of IV and III is still greater.

When further we look at the fourth digit in fig. 130, h, we see that phalanx 3 had to be drawn longer than the rest in order to correspond with the long pad. As far as I know, a long phalanx in the middle of the fourth toe is a hitherto undiscovered phenomenon (see fig. 126). The first, proximal, phalanx is the longest in all three toes, in the fourth the phalanges shorten uniformly towards the distal end. The phalanges of the fourth digit of *Anchisauripus sillimani* (fig. 130, f) do not, by the way, seem to be correctly drawn either, this footprint being ascribed to *Anchisaurus colurus*.

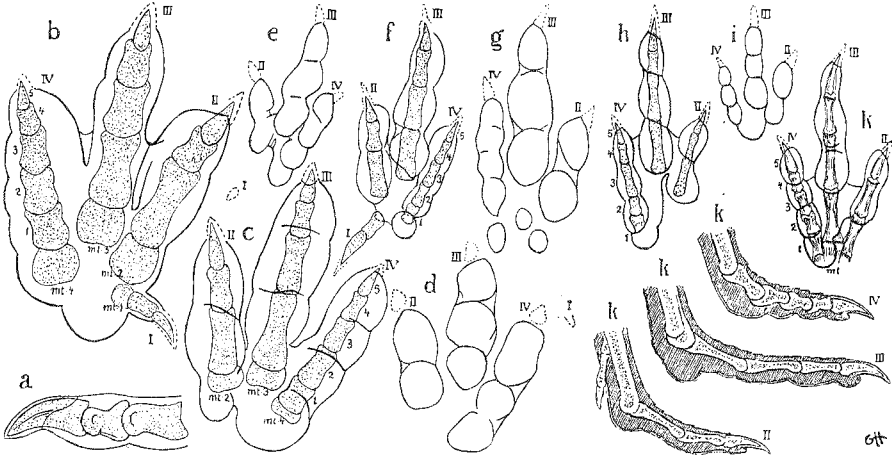


Fig. 130. a Digit II of *Dimodonsaurus*, viewed in profile with the outline restored. Footprints of Carnivorous Dinosaurs from the Triassic of Connecticut; in b, c, f, h and k the phalanges are drawn so as to show the relation of the claws and pads to the phalanges, b *Gigandipus caudatus*, c *Eubrontes giganteus*, d *E. platypus*, e *Anchisauripus hitchcocki*, f *A. sillimani*, g *A. parallelus*, h *Grallator cursorius*, i *G. gracilis*, all after R. S. Lull; k *Grallator tenuis* with the digits of *Procompsognathus triassicus* inserted, drawn by the author, and the toes of same seen in vertical, longitudinal section.

Apart from the dimensions, these *Grallator*-footprints are unusually homogeneous, and fortunately we know the foot of a Coelurosaur from the Triassic whose whole character exactly matches these tracks. It is *Procompsognathus triassicus* (fig. 126, A), and I have therefore drawn its toes fitted into *Grallator tenuis* (fig. 130, k). This gives quite a different view and, be it noticed, the toes articulate well with the closely appressed metatarsals. As these are raised a little from the ground, phalanx 1 in the figure will appear a little shorter, and I have therefore also drawn each of the three toes as vertical section, in lateral view. In this way the exact position of the pads is also plainly seen, approximately, but not exactly, opposite the joints.

The footprint, moreover, shows that there has been a foot-pad nearly under the united digits IV and III with their respective metatarsals; this also appears in the sections. Such a foot-pad is also found in our Common Fowl, whose foot I have drawn in fig. 131, J, viewed from below, and besides, each individual toe in longitudinal section.

In the Common Fowl, moreover, do the toe-pads also lie nearly, but not exactly, opposite the joints. Its foot-pad, too, belongs chiefly to digits IV and III. Apart from the greatly shortened phalanges in the fourth digit of *Procompsognathus*, the resemblance to same is very strong. The very fold of skin, which may be found between the toes of birds (fig. 131, J and H), is also seen in the two *Grallator*-footprints (fig. 130 h and k).

Nevertheless I do not consider *Grallator* the footprints of birds, for it is out of the question, I suppose, that in the Triassic there should be birds with

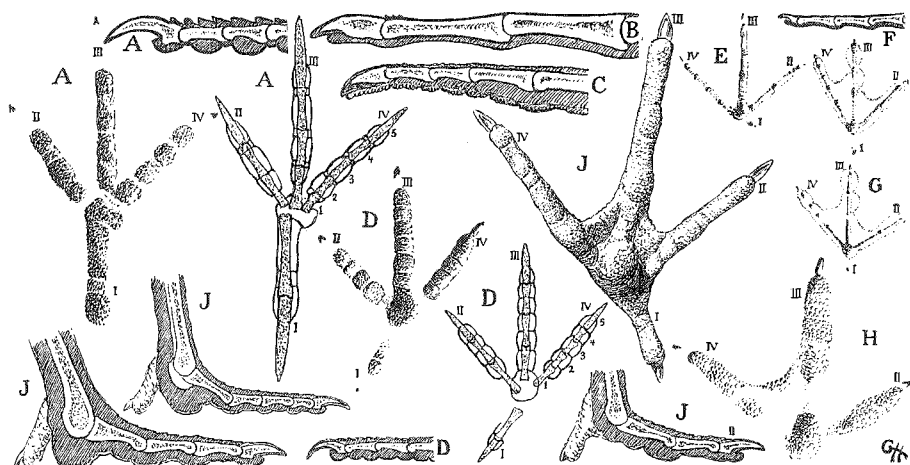


Fig. 131. Footprints of birds in soft clay and vertical, longitudinal sections of single toes. A Rook (*Corvus frugilegus*), B Swan (*Cygnus*), C Stork (*Ciconia alba*), D Pigeon (*Columba domestica*), E Dunlin (*Tringa alpina*), F Grey Phalarope (*Phalaropus fulicarius*), G Red-necked Phalarope (*Phalaropus hyperboreus*), H Oyster-Catcher (*Hæmatopus ostreologus*). In footprints A and D the phalanges are inserted. Section F slightly enlarged. J Foot of a Common Fowl, seen from below and the three single toes in vertical, longitudinal sections.

an already degenerated first toe, seeing that the Jurassic birds had a very well developed hallux, posed in level with the other toes (fig. 114, 5).

The only real difference seems to be the angle between the second and the fourth toe, which is considerably more acute (30° — 45°) in the footprints from the Trias than in recent birds, who live and move on the ground only (90° or more). We cannot, however, attach too great importance to this point, for possibly the corresponding angle in the first existing birds may have been just as acute.

A peculiarity of these footprints is that they never show the animals in a position of rest, as we found it in the case of the *Predentates* (fig. 112, B). It is but reasonable to think that it would also be natural for these *Theropoda* and *Coelurosaurs* in a sitting posture to rest on the whole foot, the tail touching the ground. We might imagine the small *Compsognathus* resting on the side with legs stretched out like a Kangaroo; it is more difficult for me to conceive of *Struthiomimus* doing the same.

This most peculiar shoot on the stem of the Coelurosaurs has several times been alluded to, and fig. 132 gives a restoration of its exterior. Apart from the tail, the animal most of all suggests a long-legged, long-necked Struthious bird, and its mode of progression has no doubt been corresponding. There is hardly anything left of genuine reptilian features. Several authors have made suggestions as to the possible use of the strongly specialized hand of *Struthiomimus* (fig. 19, VI), some saying that it was evidently for the pulling down of branches and fruit of trees; however, this might be done by a long-armed monkey or a short-necked man, hardly by an animal with a neck outstripping the arms in length; it would be easier to pick the fruit with the beak. It has also been supposed that they were adapted to scraping out and stealing large reptiles' eggs, hidden in the ground. Contemporary small mammals, we should think, would be better adapted to burrowing of that kind. That the heavy claws might "have been useful in tearing off the husks of fruits", as suggested by W. K. Gregory (23), sounds more probable. But all this is mere guesswork, until a good find shall enable us to say something of the contents of the stomach. Were it not for those peculiar arms, our nearest guess would be that it was omnivorous like the Ostrich.

The above mentioned facts go to prove that in Coelurosaurs the likeness to birds is greatly on the increase throughout millions of years, thus in marked contrast to the Predentates in which these features are gradually diminishing. And further, while the striking points of similarity between Coelurosaurs and birds pertained to nearly all the parts of the skeleton, it was in the Predentates mainly the tarsus which retained some likeness to that of birds. From this it would seem a rather obvious conclusion that it is amongst the Coelurosaurs that we are to look for the bird-ancestor. And yet, this would be too rash, for the very fact that the clavicles are wanting would in itself be sufficient to prove that these saurians could not possibly be the ancestors of the birds.

That flying is possible without a clavicle, to be sure, we learn from the Pterosaurs, but that this bone belongs to the original bird-skeleton will appear evident from its presence in both the Jurassic birds, and it is even found in the wingless *Hesperornis regalis* (fig. 8, H). Consequently, a bird-ancestor could not be without clavicles.

On going through the various points of resemblance to birds, moreover, we shall find that they denote less affinity to the Jurassic birds than an evolutionary tendency parallel to the development of some birds that have left off flying and in some respect are degenerate.

We need not lay much stress on the tendency to toothlessness, for we find the same thing within several other groups of reptiles. But the cervical ribs, from being loosely attached, become shortened and closely coalesced to the sides of the cervical vertebræ. The sternum resembles that of very degenerated Struthious birds, which also may be said of the foot. The three metatarsals do not lie in the same plane as they do in the Jurassic birds, but they bear the same relationship to one another as obtains in recent birds. The phalanges of the toes, especially the fourth, are much more shortened, and the first

metatarsal and first digit are no more on a level with the others, for which reason the footprints show no hallux-impression.

As seen in fig. 19, the fore-limb strongly reminds one of the wing-skeleton of *Archaeornis*, more than that of any other reptile; and although such an

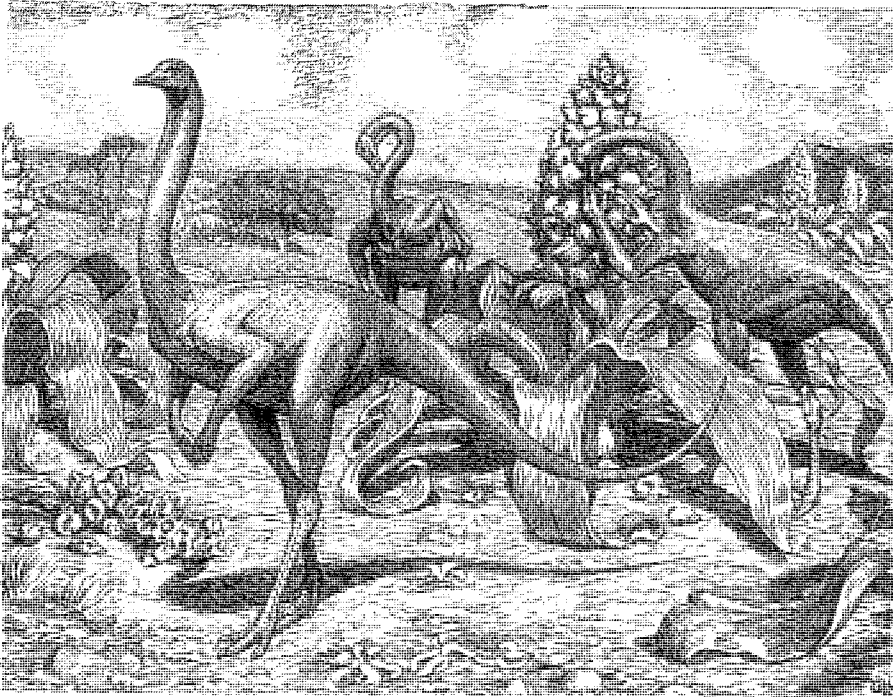


Fig. 132. Restoration of *Struthiomimus altus* from the Cretaceous by the author.

instance in itself cannot be conclusive, yet it seems to show that a rather close kinship exists between Coelurosaurs and birds, even if several points of resemblance in the rest of the skeleton may be due to analogous adaptations owing to the same bipedal mode of progression.

We have therefore reasons to hope that in a group of reptiles closely akin to the Coelurosaurs we shall be able to find an animal wholly without the shortcomings here indicated for a bird-ancestor.

PSEUDOSUCHIANS

Such a group is possibly the Pseudosuchians, by several authors, especially F. v. Huene (11 and 16), considered the ancestors of the Theropodous Dinosaurs and Coelurosaurs. I quote from R. Broom (28), as follows: "In fact there seems to me little doubt that the ancestral Dinosaur was a Pseudosuchian. The skulls of such types as *Euparkeria* and *Ornithosuchus* are practically Dinosaurian even in detail, and the skulls of the early Dinosaurs, such as

Anchisaurus, differ less from the skulls of Pseudosuchians than those of the early do from many of the later types. And there is nothing in the post-cranial skeleton that is not just what we should expect to find in the Dinosaur ancestor". F. v. Huene thinks that from the Proterosuchians, i. e. primitive Pseudosuchians from the Lower Triassic, did the first Coelurosaurs originate.

For our subject, then, this means that all the bird-like features we met with in the Coelurosaurs may be considered as a further development of some of the possibilities inherent in the Pseudosuchians.

Our study of the Coelurosaurs and especially of the Predentates gave ample proof that from no stock of animals strongly specialized in a certain direction can forms arise showing a tendency to a specialization in quite another direction. I refer to Dollo's law of irreversible evolution alluded to at the beginning of this part.

Before following up our subject we shall try to make intelligible to ourselves what to expect in an animal eligible to be the bird-ancestor.

Its braincase must have been small, and its cranium would show an intensity of the reptilian features found in the skull of *Archaeornis*. There will thus be a very distinct supratemporal fenestra, and there will be no break between the squamosal and the quadratojugal, the infratemporal fossa being entirely surrounded by bone. The quadrate of course immobile, and a transverse bone present; further, a large orbit with a sclerotic ring and a well developed preorbital fenestra; conical teeth implanted in distinct sockets. The vertebræ with slightly concave or plane anterior and posterior surfaces, but their number cannot be stated in advance because of its variability even in species closely akin; in a bird ancestor we may possibly find a similar number as in *Archaeornis*. There need, however, be only two sacral vertebræ as preformed in the bird-embryo. We must of course look for a long tail, ribs, perhaps with uncinatè processes, and ventral ribs. The shoulder-girdle must be wholly without defects comprising both clavicles, episternum, and perhaps suprascapula, a preformation of this bone being found in the bird-embryo. The pubis most likely still directed forward, but probably commencing to turn backwards. The hand with 3—4 digits. The foot with distinct metatarsals, not at all specialized, and 4—5 digits.

In going over the skeleton of the Pseudosuchians, we shall see whether it complies with the requirements in question.

In Part I we have already compared the skulls of two Pseudosuchians with that of *Archaeornis*, and I here submit the figure once more (fig. 133). The resemblances are exceedingly striking; there is practically no difference at all. If we compare the individual bones one by one, we shall see how in shape, dimensions, relative positions, etc. they are, to all intents and purposes, alike in the two Pseudosuchians and the Jurassic birds. Their resemblance is so thorough that even the directions of the sutures between the individual bones are the same, and have remained unchanged down to the present time (fig. 133, E). Also a large preorbital fenestra and orbit are found in these Pseudosuchians. "There are well-developed sclerotic plates in the eye, which

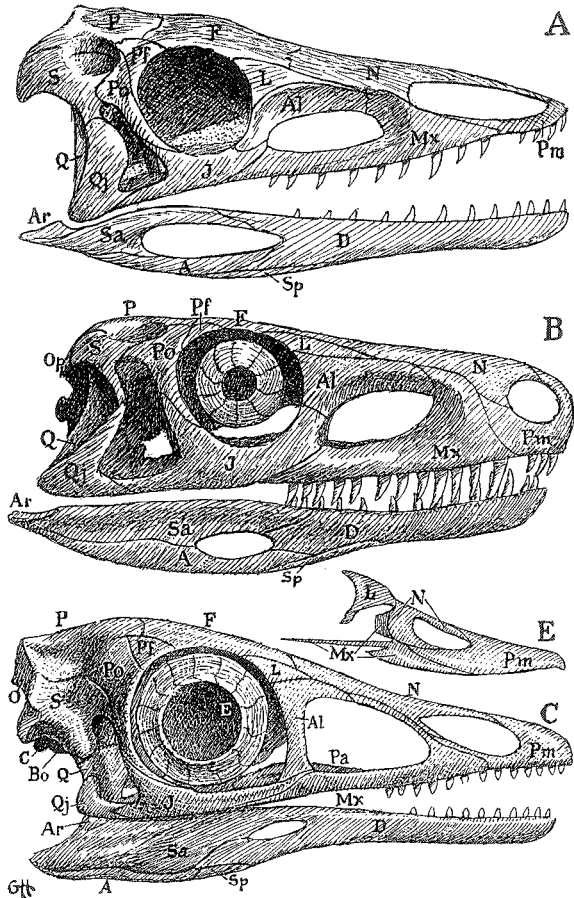
Fig. 133 Right side-view of the skull A of *Aëtosaurus ferratus* from the Triassic, after F. v. Huene; B of *Euparkeria capensis* from the Triassic, after R. Broom; C of *Archaeornis siemensi* by the author; E upper jaw of Pochard-duckling (*Fuligula ferina* juv.). Lettering as before.

are curved as in the bird" (28). "The premaxilla supports at least two and most probably three flattened, pointed thecodont teeth", and the maxilla has 13 thecodont teeth of the same form. The teeth of *Archaeornis* are also thecodont, and they were likewise to be found in the premaxilla (fig. 133, C).

In fig. 31 was shown that in the skull of a young bird the occipital condyle is composed of elements from both the exoccipitals and the basioccipital. It is therefore of some importance that the same thing is to be found in the Pseudosuchians. R. Broom writes about *Euparkeria* (28): "The exoccipital forms part of the occipital condyle and passes outwards, fusing with the opisthotic. Only a small part of the basioccipital shows in the specimen as the middle part of the condyle".

"A pair of long rib-like bones represent portions of the hyoid apparatus. These are evidently the ceratobranchials, and indicate that *Euparkeria* had a birdlike tongue" (28). In fig. 6 we compared the skulls of *Euparkeria* and *Archaeornis* in top view. The resemblances were also here striking. The small interparietal, seen in *Euparkeria*, is also to be found in birds, for instance in the skull of the Rhea; in fig. 31, 2 we see it in the skull of a gosling. The little bone, by the way, is not a constant feature in the Pseudosuchians; it is wanting in *Ornithosuchus*.

For the ventral aspect of the skull we have been unable to institute any comparisons, this part of the *Archaeornis*-cranium not being accessible for investigations. And so in fig. 134, A, I have represented the palate of a Kiwi in order to compare it with that of *Ornithosuchus*, of which only the basioccipital region is somewhat hypothetical. "The palate of *Ornithosuchus*



woodwardi is well preserved". "The skull, on the whole, resembles that of *Euparkeria* in all essentials, so far as can be seen" (28). The Pseudosuchians, of course, offer more original, hence less specialized, forms of the individual bones than the Kiwi; otherwise the position of the bones is nearly identical. "The pterygoid sends forward a long slender process along the inner side of the palatine which doubtless meets the prevomer as suggested in the figure"

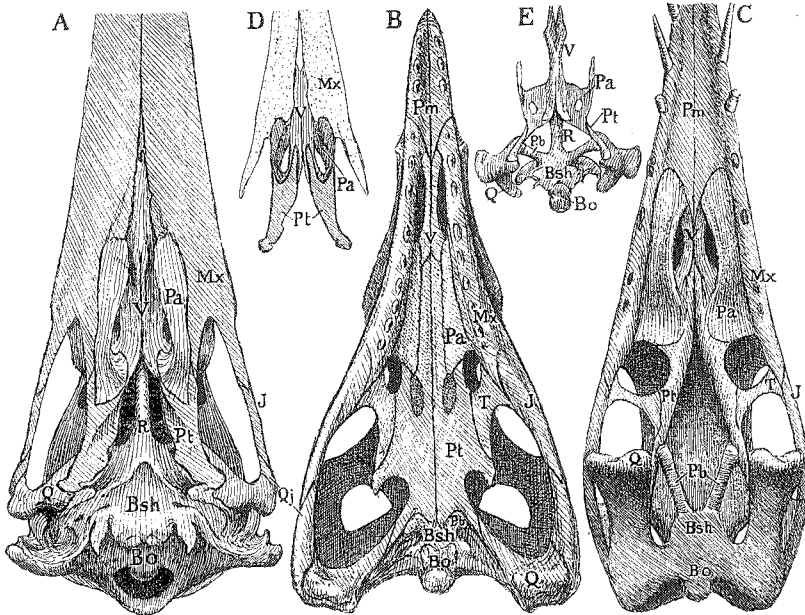


Fig. 134. Skulls in palatal view of a Kiwi, *Apteryx australis*, after Pycraft, B *Ornithosuchus woodwardi* from the Triassic, after R. Broom and E. T. Newton, C *Ramphorhynchus gemmingi* by the author, after A. S. Woodward and F. v. Huene; D palate of Kiwi in dorsal view, after Pycraft, E palate of Rhea, after Pycraft; Pb basipterygoid process, T transverse bone. Lettering as in fig. 3.

(28). In order to show that the same thing holds true of the bird, I have represented the palate of the Kiwi as seen from above in fig. 134, D; a process from the pterygoid also here meets the vomer (prevomer).

In Part I we made mention of the strong basipterygoid processes articulating with the pterygoid in *Hesperornis* (fig. 29, 1 and fig. 31, 1 Pb), and the same processes are also found in *Ornithosuchus* (fig. 134, B, Pb). In the Rhea, too, these are very conspicuous (fig. 134, E, Pb), and in the palate of a long-tailed Pterosaur seen in the same figure. These two processes (Pb) are vanishing in the birds, but found in their embryos and young ones, even when they have entirely disappeared in the adult bird. Consequently, they belong to characteristic features of the past.

The palate of the Pterosaur shows exactly the same position of the palatine in relation to the vomer as we saw in the Kiwi, and the pterygoid sends forward a process to meet the vomer. The transverse bone (T) became superfluous in birds, hence it has vanished in their case.

In the Pseudosuchian skull, therefore, we find nothing whatever to contradicts the supposition that the avian ancestor was a Pseudosuchian.

Euparkeria has 9—10 cervical vertebræ, *Archaeornis* had 10—11. "They are amphiplatyan or incipiently procæalous; there are 2 sacral vertebræ and apparently 26 presacrals" (28). Most likely *Archaeornis* had biconcave vertebræ, 4 sacrals and about 25 presacrals. As in birds "the ribs are double-headed and have small uncinæ processes (fig. 68, 4), firmly attached to the posterior side of the ribs but not ankylosed" (28). In *Hesperornis* the uncinæ processes had not yet fused with the ribs (fig. 66, 4); the same is the case with those of the Kiwi (fig. 66, 5). "The tail is very long (in *Euparkeria*) and has powerful chevrons": *Ornithosuchus* had 3 sacral vertebræ and 8 cervicals.

"There is a large broad plastron of abdominal ribs. The riblets are all slender and arranged in series of threes — a long outer riblet, a shorter middle one, and a still shorter inner one" (28).

"The shoulder-girdle is well preserved. There is a long slender interclavicle; the clavicle is also long and slender" (28). The coracoid has a large oval foramen. In fig. 68 we have already seen how close the resemblance was be-

tween the shoulder-girdle of *Euparkeria* and that of the bird-embryo in regard to the connection of the clavicle, scapula, coracoid, and episternum (interclavicle). And this was so fully explained in the text that it is unnecessary to add any more. The shoulder-girdle of the Pseudosuchians consists of exactly the same elements as that of the birds and could easily change into same. As an essential difference from the groups of reptiles mentioned before, we particularly wish to emphasize the well developed clavicles in the Pseudosuchians.

Fig. 135 shows the shoulder-girdle of *Ornithosuchus* in connection with arm and hand, which are rather primitive in every respect. Of the hand only a part of the three fingers remains; and Broom writes (28): "There are pretty certainly three well-developed digits, and, I think, evidence of a fourth. The

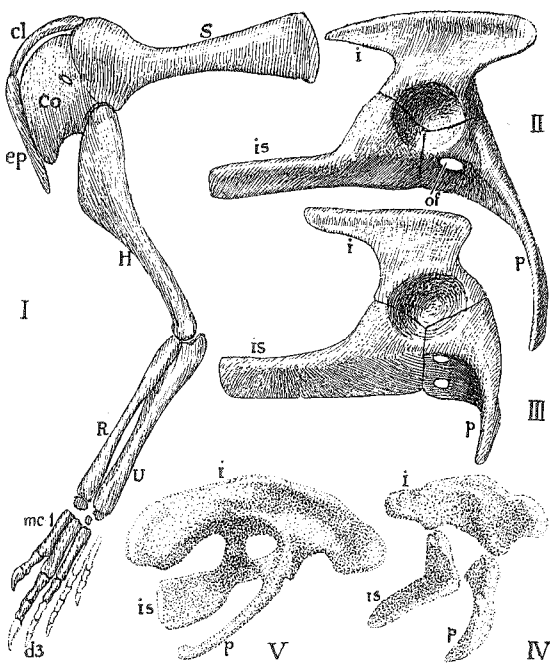


Fig. 135. I Shoulder-girdle and fore limb of *Ornithosuchus woodwardi* from the Triassic after R. Broom and F. v. Huene, II pelvis of same, III pelvis of *Euparkeria capensis* from the Triassic both after R. Broom, IV and V embryonic pelvises of IV Black-headed gull, *Larus ridibundus*, V Common Fowl, both after N. G. Lebedinsky. Lettering as before.

carpus is badly preserved: possibly it was imperfectly ossified". Yet three carpals are found, as shown in fig. 135, I, most likely ulnare, radiale, and a distal carpal. Neither in *Euparkeria* nor in *Saltoposuchus* (16) is the hand preserved, but F. v. Huene's reconstruction of the latter appears in fig. 122, 1. This figure shows, on the whole, how the arm and hand of the Pseudosuchians, passing transitional stages, probably resembling the corresponding forms in the Coelurosaurs, might easily change into the fore-limb of *Archaeornis*, the second digit becoming the longest, while the fifth and the fourth digits vanished.

In the pelvis of these Pseudosuchians (fig. 135, II and III) it is mainly the pubis that excites our interest. For it has a rather peculiar, twisted form; it looks as if it were about turning backwards, thus exactly fulfilling our expectations as to the pubis of a bird-ancestor. We see, as it were, the beginning of the pelvic evolution of the bird-embryo. For the sake of comparison I have therefore in the same figure represented two embryonic stages of bird-pelves, thus rendering the transition from the pelvis of the Pseudosuchians to that of the bird the more conspicuous. The acetabulum is closed in the *Pseudosuchians*, and in *Archaeopteryx* it "is partly closed by a thin marginal lamina of bone, which is preserved at its anterior border" (29); hence, a transition to the perforate acetabulum in birds. In the Pseudosuchians there is a pubic as well as an ischia-symphysis; *Archaeopteryx* had retained its pubic symphysis, while that of the ischia was lost.

On the inner and posterior side, near the union of the upper and middle third, the femur of *Euparkeria* has a well-marked fourth trochanter. The femur of *Saltoposuchus longipes*, too, bears a fourth trochanter (16). The tibia and fibula are well preserved in the various Pseudosuchians. "The tarsus consists of two proximal elements, and probably four distal tarsals" (28). The entire tarsus foreshadows that of the birds. The metatarsals are all well developed, and in *Saltoposuchus longipes* they are very elongate (fig. 122, 1). It is worthy of notice that the third metatarsal and the third toe are the longest, which means that the elements of the foot were already beginning to arrange themselves round the median line just as in the bird's foot. Otherwise it is in reptiles generally the fourth toe that is the longest.

A and 1 of fig. 122 show the entire hind-limb of two Pseudosuchians, and looking at the hind-limbs of the Coelurosaurs we may imagine the process of transformation into that of a bird. The greatest change that took place was the loss of the fifth toe.

Broom's (28) opinion about *Euparkeria* is that it was "potentially bipedal, and was probably partly bipedal in its habits. The fourth toe of the hind foot is more feebly developed than the third and the axis of the foot is down the third toe, which would seem to indicate that the feet were at least not so laterally placed as in lizards, and that the animal possibly ran on its hind feet. The relative shortness of the toes also seems to confirm this view as well as the feebleness of the fore-limbs". "*Ornithosuchus* was probably very similar in habit to *Euparkeria* and was even a little better adapted for running

on its hind feet". F. v. Huene (16) imagines the locomotion of *Saltoposuchus longipes* as half erect, running on the hind legs, the comparatively small fore-limbs being incapable of supporting the body.

In fig. 136 I have drawn the skeleton of *Ornithosuchus* in such a running position. From this the contour of the animal could then be supplied and a plastic model formed, from which again I have drawn fig. 137. Also from the exterior of the Pseudosuchian we see how little specialized the animal is; only the rather short toes, the somewhat longer metatarsus, and the position of the bones give evidence of a divergence from the ordinary type of reptiles. But it is light in structure and nimble in movement, as we should expect to be the case in a bird-ancestor and the tapering head is very bird-like. We need

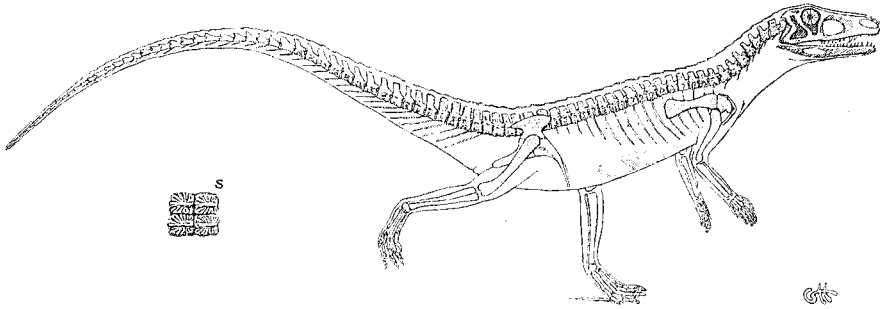


Fig. 136. Restored skeleton of *Ornithosuchus*, after E. T. Newton, R. Broom and F. v. Huene; s four isolated scales of same.

only compare it to the heavy and clumsy *Iguanodon* (fig. 111), which nothing but sheer misconception as to the fundamental laws of descent could possibly have placed amongst the ancestors of the birds.

All these Pseudosuchians were covered with scales, and in *Euparkeria* "all the best preserved scutes are about twice as long as broad and have the long axis lying antero-posteriorly" (28). From this axis there are distinctly traceable ribs running sideways (fig. 136, s), in form almost representing a feather; we need merely imagine the ribs continued beyond the border of the scale.

From the investigation we here have set on foot, it is evident that all our requirements of a bird ancestor are met by the Pseudosuchians, and nothing in their structure militates against the view that one of them might have been the ancestor of the birds. This of course does not prove that this ancestor was one of the known Pseudosuchians. It is possible that later finds shall furnish us with a Pseudosuchian still more akin to the genus of birds; it would be a stroke of good luck, hardly to be expected, if, amongst the many thousands of reptile species living in the Triassic, the very ancestor of the birds should have been preserved.

Several authors have already called attention to this derivation from the Pseudosuchians, and although more than once in the preceding pages we have seen how misleading such statements may be when unsupported by a thorough comparison of the various parts of the skeleton, I shall here quote

from R. Broom (28), as follows: "The *Pseudosuchia*, now that it is better known, proves to be just such a group as is required. In those points where we find the Dinosaur too specialized we see the Pseudosuchian still primitive enough. The bird pelvis has probably developed from a type like that of *Ornithosuchus* by the pubis turning further back and the symphysis becoming lost. Whether the union of the metatarsals is a primary or secondary character is a debatable point. The question is really whether the bird ancestor

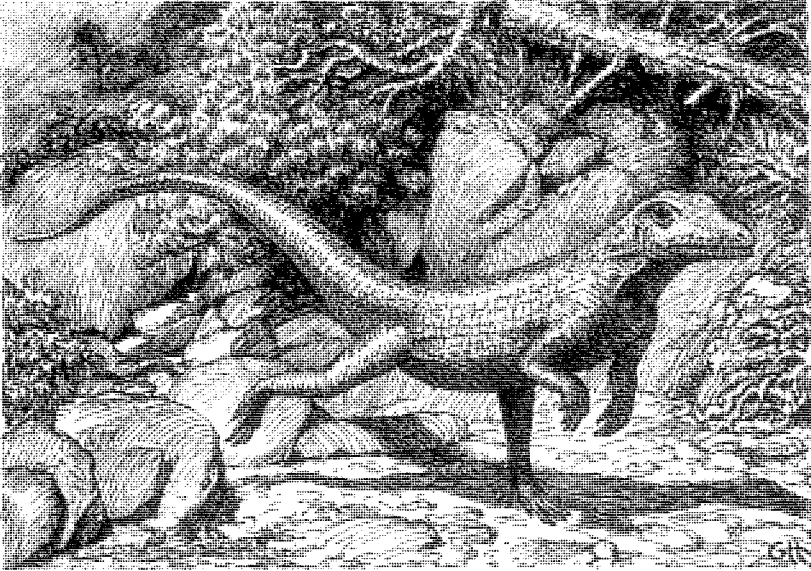


Fig. 137. Restoration of *Ornithosuchus* by the author.

was a hopping bipedal animal before it flew, or if it only hopped after the wing had become specialized. I am strongly of the opinion that it was a hopping animal first, and that the metatarsus became strengthened to support the weight of the body entirely borne by the hind feet. It is easy to understand a hopping animal taking to an arboreal life and ultimately developing a wing out of a four-toed hand, while it seems unlikely that the hind foot could ever have developed by arboreal habits". "A Pseudosuchian which through a bipedal habit had developed a strengthened ankle-joint and a firm metatarsus, and had lost the fifth digit from the manus would meet all the requirements of the avian ancestor".

The transition from such a Pseudosuchian towards the Proavian must have taken place by a lengthening of the hind-limb, especially the metatarsus and possibly the toes, of the fore-limb, especially the hand, and of the neck, and by a shortening of the tail. Moreover, by a transformation of the skull and a turning backward of the pubis, the symphysis being retained.

As to the time of these changes, we cannot venture to suggest anything even approximately correct. *Saltoposuchus* was contemporary with *Procomp-*

sognathus in the Upper Triassic, and the departure of the Coelurosaurs from the Pseudosuchians must therefore have taken place much earlier, possibly at the beginning of the Trias (F. v. Huene, 16), and perhaps the development of the Proavian was started during the same period.

R. S. Lull (19) thinks that the bird stock arose already in the Permian, the climate at that time being arid or semiarid, which would be conducive to an accelerated speed of the animals. Further, there also occurred an extensive glaciation with a severity of climate, especially in the southern land masses, and with warmer interglacial intervals. "The incentive for speed already given, rendering the development of warm blood possible, the devastating cold would soon place a premium upon such as did develop it and eliminate those which did not. From this fortunate relation of cause and effect arose . . . the ancestral bird" (19, p. 307). To this we may object that, in all probability, warm blood was not aquired at so early a stage, long before the feathers as yet could have started to develop. There are also other points of great importance to this development, which could not be explained by these climatic conditions, and which we shall take up in the following pages.

THE PROAVIAN

The term Proavian or Proavis covers a form intermediate between reptile and bird; hence, a form that is no more a reptile, but which has not as yet become a bird. We must suppose the animal to be partly covered with scales, but these are in certain places beginning to change into feathers.

Being proved conclusively that the bird was derived from the reptile, it is obvious that such an intermediate form at some time must have lived, and although the remains of same are still wanting amongst fossils, we should like to know something more definite about this strange creature.

A purely fanciful image we can always conjure up, but in setting out to find the Proavian, we wish to tread on more solid ground. For it is a veritable exploratory expedition into the obscurities of the past. In our eager look-out for the goal we are unable to gain any distinct idea of the animal. From our large stock of materials for comparison, some particulars of the skeleton may dimly stand out, but as a whole our vision is blurred. We must therefore stick to the individual parts of the skeleton, then proceed to build up the whole thing, until at length we gain a distinct impression of this strange intermediate form.

First of all we direct our searchlight towards the cranium. We are familiar with the skulls of *Ornithosuchus* and *Euparkeria*, and draw up a skull in side view intermediate between these two. This profile, when placed side by side of that of *Aëtosaurus*, supplies us with a new profile drawing, some type of a Pseudosuchian skull. The form intermediate between this one and that of *Archaeornis* will come out by a rather simple mathematical construction: In the first place, one of the skulls is squared, and the other skull is

fitted into a corresponding network of co-ordinate lines. Next, an empty network is drawn, just intermediate between these two, and in this the outline of the desired skull may easily be filled in (30, p. 765—768).

The skull in top view may be drawn in a similar way, and, in order to test its correctness and get it as exact as possible, parallel lines may be drawn through the corresponding points of the figures in profile and top views. For the proavian palate I had to rest content with the palate of *Ornithosuchus* as a point of departure.

Fig. 138 gives the result arrived at. The skull has still retained the transverse bone of the reptile, but it is about vanishing; the union of the squamosal and the quadratojugal has not yet been broken. And although it has diverged considerably from the original reptile cranium, it is still quite primitive, and not yet specialized in any respect.

Before starting to reconstruct the proavian skeleton, we must try to gain a clear understanding of the particular peculiarities in same that would lead on to the bird.

Already in 1900 Osborn (9) preferred a conjecture about a "Dinosaur-Avian stem", and urged an arboreal origin of flight. In 1911 O. Abel (31) pointed out that "the opposability and turning backwards of the hallux, as also the strong bending of same, cannot possibly be otherwise considered than a phenomenon incident to the arboreal life". And further: "The considerable difference in length between fingers and toes in *Archaeopteryx*, which has been inherited by more recent birds, is an acquisition during the arboreal life of the ancestors", and that the reduction of the digits of the hand together with the predominant elongation of the second digit is not a special acquisition of the birds, but a feature common to all Theropoda and birds. His conclusion is (31, p. 190) "that the birds and the Theropoda are descended from a common arboreal stem group with climbing feet, from which the Theropoda, for their part, at an early period returned to a terrestrial mode of life, while for the birds, which remained arboreal, the return to terrestrial life did not take place till a long time after the faculty of flight was acquired. And a further consequence, derived from the first, is the conclusion that the birds and the Theropoda diverged at a very early period, probably at the beginning of the Triassic epoch".

It is no doubt correct that the acquisition of a hind-toe is due to arboreal habits, possibly this also has caused the complete reduction of the two ulnar digits of the hand and the elongation especially of the second, but it does not hold true in all cases. For the foot of *Procompsognathus triassicus* (fig. 126, A) proves beyond a doubt that its hallux has been an oppositive hind-toe. Its ancestors, therefore, have acquired same by climbing the trees, but its hand (fig. 124, I) has remained a primitive pentadactyl, there is no reduction of digits and no predominant elongation of the second one.

From this we must infer that at least some groups within the Coelurosaurs and Theropodous Dinosaurs have left the trees before any transformation of the hand was commenced, while others have remained longer in the trees

Fig. 138. Skull of the hypothetical Proavis in side, top and palate view, reconstruction by the author; lettering as in figs. 3 and 133, T transverse bone.

and thus attained a more pronounced specialization of the hand.

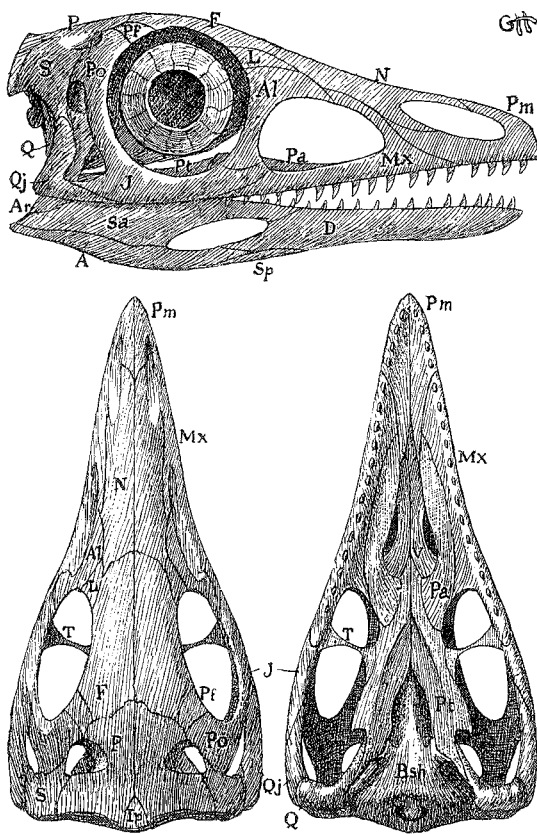
In this way I think that both *Ornitholestes* and *Struthiomimus* owe to their arboreal ancestors their tri-dactyl hand with the special elongation of the penultimate phalanges, which has been retained after the animal returned to a cursorial life.

This elongation of the penultimate phalanges, which is also a special characteristic of *Archaeornis*, was already alluded to in connection with fig. 19, and we must presume that the Proavian, once having commenced living in trees, had already developed a hind-toe and a specialized hand with a long second digit and elongate penultimate phalanges. This is therefore to be borne in mind when we go to the construction of the Proavian skeleton.

The theory of a not arboreal, but wholly terrestrial "running Proavis", urged by some authors (32), cannot, according to the above facts, be sustained. We have learned, moreover, that the hallux in bipedal, terrestrial animals, as a rule, vanishes entirely, and that the fore-limb, instead of being elongated, most frequently is reduced in size.

For our starting-point in the reconstruction of the proavian skeleton we have the almost complete skeletons of *Aëtosaurus*, *Euparkeria*, *Ornithosuchus* and *Saltposuchus* on the one hand, and those of the Jurassic birds on the other. Consequently, we can reconstruct the individual bones separately, one by one, and of these elements compose the skeleton. Fig. 139 gives an idea of how it might have looked.

The skull is rather large, in proportion to the rest of the skeleton, but the cranium of the Pseudosuchians is also much longer than for instance that of the Coelurosaur. Possibly the hind-limbs have still retained some of the position seen in the reptile, and the femora may not have been fully directed forward. The tail is long, but the elongation of the hand is not yet conspicuous.



The pubis is beginning to turn backwards. The proximal part of the first metatarsal is still present, but about vanishing. For the reconstruction of the hind-limbs I have especially used those of *Saltoposuchus longipes*. — To preclude any misunderstanding, I shall add that we have no fossil record of such a skeleton as represented in fig. 139.

By drawing up the outline of the body, around the skeleton, we are furnished with a basis on which to construct a plastic model of the animal. Before arriving at this result, however, there are still some particulars to be considered.

C. William Beebe (33) has drawn a sort of Proavis in a "tetrapteryx stage" with "pelvic wings", as he calls them, mainly based upon an observation "of sprouting quills across the upper part of the hindleg" "of a four-day's-old White winged Dove". He states "that this was no irregular or abnormally precocious development of part of the femoral pterygium, but a line of primary-like sheaths", containing twelve flight feathers, of which the six proximal ones "all have a well-developed covert" (fig. 140, 1 and 2).

Beebe has further examined four squabs at differing ages of the domestic pigeon, with the result that the "pelvic wing" as a matter of fact is the lasting thigh feathers; besides, a semi-developed embryo of the Jacana in which "the rectrices and pelvic alar feather papillæ are well ahead of all others, even of the wing proper".

Literature on *Archaeopteryx* does not furnish us with any definite answer to the question whether its thigh feathers were of any importance to its flight, the different statements being both pro and contra. For this reason Beebe has examined a photograph of the specimen in Berlin, and gives the following result of his investigations: "It seems reasonable to me that this group of feathers, which somewhat resembles a diminutive wing, may represent the pelvic alar tract which is so remarkably developed in modern squabs" (33). And he thinks the function of the pelvic wings both in *Archaeopteryx* and in the prejurassic Tetrapteryx to have been merely passive parachutes, becoming more and more reduced in succeeding generations.

He sums up by the following ingenious argument: "Millions of years after they were of use, the feathers of the pelvic wing are still reproduced in embryo and nestling. And for some unknown reason, Nature makes each squab pass through this tetrapteryx stage. The line of feathers along the leg of the young bird reproduces on this diminutive, useless scale the glory that once was theirs. No fossil bird of the ages prior to *Archaeopteryx* may come to light, but the memory of Tetrapteryx lingers in every dove-cote". It is thus beyond a doubt that he considers these "femoral quills" of the squab a relic from the past.

This observation is of course bound to interest every ornithologist, and it was therefore with some excitement that I began to study the great number of small nestlings at the Zoological Museum in Copenhagen. Unfortunately it resulted in a complete disappointment, for what I found was wholly negative; there was not in any of them the slightest trace of a "pelvic wing".

Hoping that this feature would stand out more distinctly in the lowest

birds, I first examined the young ones of Ostrich and Emeu; but in their downy coat there was not the slightest trace of sprouting quills on the hindleg. The same thing was the case with the different species of Divers (*Colymbus*) and Grebes (*Podiceps*), Ducks, Auks, Birds of Prey, Storks and Herons, Terns and Gallinaceous Birds (fig. 140, 5). In a downy nestling of the Marsh-Harrier (*Circus æruginosus*) some feathers along the sides of the body were the first to sprout.

The entirely nude embryos and downy squabs of Shags (fig. 140, 6) and Gannets evinced no acceleration of the quills of a pelvic wing; there was nothing whatever to see or to feel, and it is difficult for me to imagine that the Danish squabs should have been less tetrapteryx-like than the American ones.

Nor is this evidently the case, for in his charming book "The Bird" C. W. Beebe reproduces in fig. 10 a photograph of two Brown Pelican squabs, in fig. 36 we see them in downy plumage, but in neither of the illustrations is any trace of a pelvic wing to be detected. The same holds good of the nestling Turkey Vulture in fig. 254, the nestling Catbird in fig. 257, and the young Green Heron in fig. 258. In my fig. 83 of the nestling South-American Hoatzin there is no indication of a pelvic wing, either.

Of course, I took particular notice of the nestlings of Pigeons. An about four days old squab I have drawn in fig. 140, 3. Its downy coat is rather hair-like, and there is no indication of femoral quills whatever. Only when

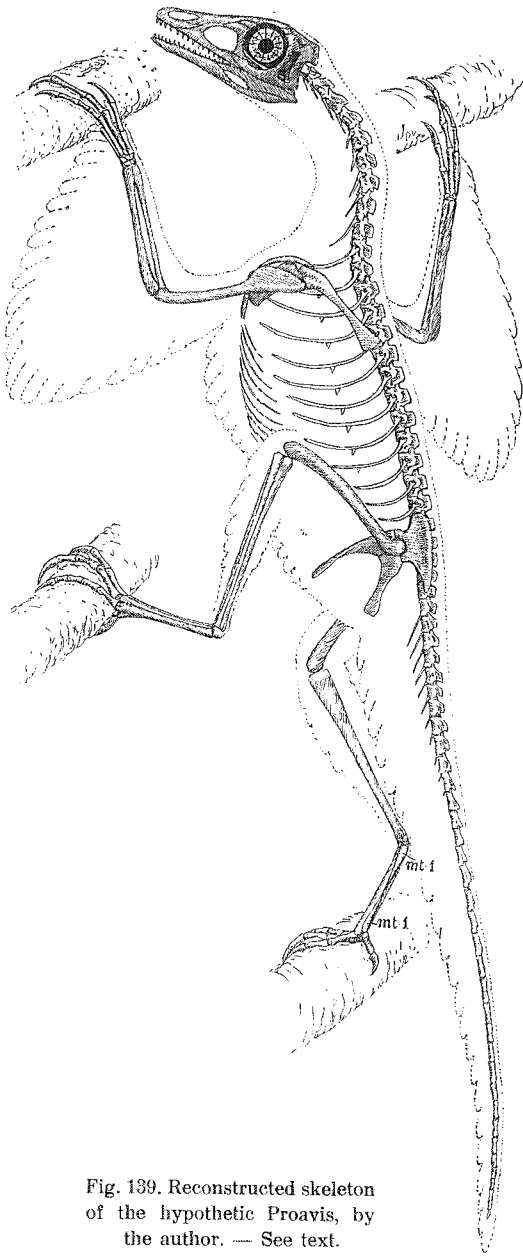


Fig. 139. Reconstructed skeleton of the hypothetic Proavis, by the author. — See text.

the permanent feathers begin to develop, they will of course sprout on the thigh as well, because normally a feathered tract is pertaining to this part. In his Dictionary of Birds, Newton names 10 principal feathered tracts and amongst these "7. Femoral or Lumbar tract (*pteryla femoralis s. lumbalis*), forming an oblique band on the outer side of the thigh". And in the illustrations, for instance that of the Green Woodpecker (fig. 140, 7), this tract is seen to form an area from the outer edge of the crus, about one-third of the distance down from the knee, extending backward across the tibia, a little posterior to the femur. Nearly in these terms does Beebe describe the place

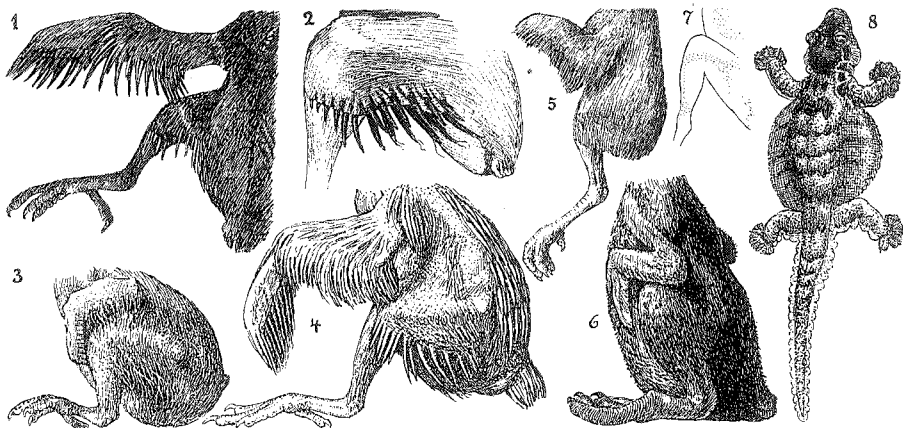


Fig. 140. 1 Four days old squab of White-winged Dove, *Melopelia asiatica*, 2 detail of same showing the pelvic wing, both after C. Will. Beebe; 3 and 4 squabs of Domestic Pigeon, 3 about four days old, 4 several days older; 5 nestling of Pheasant, *Ph. colchicus*, 6 squab of Shag, *Phalacrocorax graculus*, about ten days old, 7 hind-limb of Green Woodpecker, *Gecinus viridis*, showing the femoral feathered tract, after Alf. Newton, 8 Fringed Gecko, *Ptychozoon homalocephalum*, after Brehm.

where he has found the pelvic wing. It will also appear from his illustration (fig. 140, 2) that this is the exact spot.

My drawing of a somewhat older Pigeon-squab (140, 4) shows that the feathers of the femoral tract are sprouting together with the rest; they are here no longer than those of the spinal and of the shoulder-tract. The "pelvic wing" seems to be nothing but an abnormally accelerated development of the feathers in the femoral tract; hence, a series of permanent feathers, and no atavism. If it were a genuine relic from such a very remote past, it would make its appearance, like a glimpse, in the embryo or squab, quickly to vanish again.

As for *Archaeopteryx*, that is *Archaeornis*, its thigh feathers are, it seems to me, too weak to be called "supplementary wing feathers", but of course this is a matter of judgment. As conclusive evidence, however, I consider the position of the hind-limbs of the fossil. *Archaeornis* lying on the belly upon the slab, showing in dorsal view (fig. 2) the tail and the fore-limbs stretched out on both sides; the femora would also, as in a reptile, extend

on both sides, if the femoral wing had been of any importance to the flight of the animal. But this is not the case; we can see very plainly that they have been directed forward during the locomotion of the bird, just as they are in a recent bird. Although the skeleton of *Archaeopteryx* in London is disjointed, it is evident that originally the animal has been lying on its belly, presenting the dorsal aspect of the tail and wings, while the hind-limbs appear from the sides.

This matter is essential to an understanding of the development of the animal into a bird, for next to the wings it is the free hind-limbs that characterizes the bird as such.

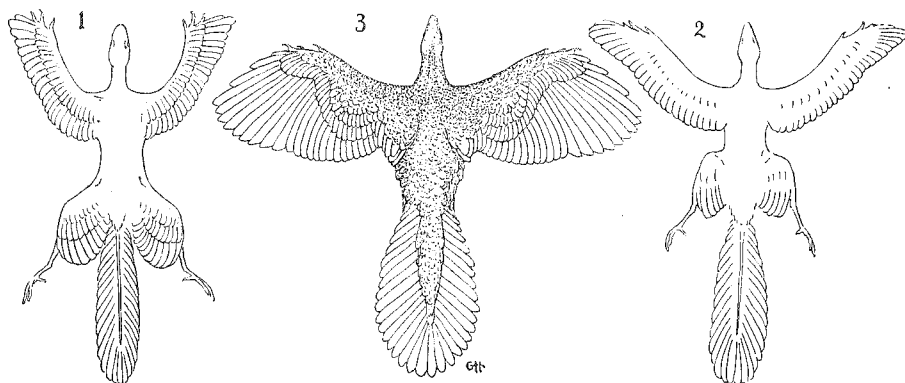


Fig. 141. 1 The Tetrapteryx stage and 2 the Archaeopteryx-like stage, both after C. Will. Beebe.
3 *Archaeornis* by the author.

To all flying animals equipped with a more or less developed patagium, e. g. Flying Marsupials and Squirrels; Cobego, Bats, and Pterosaurs, it is a characteristic feature that the hind-limbs are incorporated in the patagium, their use thus being considerably diminished, a drawback to the animal's moving about on the ground or in trees. In this respect they constitute an absolute contrast to the birds, and in our study of how the original parachute of the bird has developed, these animals give us no aid to an understanding of same.

The animal with which we may best compare the bird-ancestor, is the Fringed Gecko, illustrated in fig. 140, 8. This arboreal Gecko has, by downward leaps, developed expansions of skin wherever the air most grazes the body in its downward motion, that it to say, on the sides of the throat, trunk, and tail, and along the hind margins of the limbs. The limbs have thus retained their mobility, not being hindered by any patagium, which would tie them to the side of the belly.

A similar evolution we must imagine for the bird-ancestor; consequently, I should not think it impossible that the Proavian also had elongate, feather-like scales on the posterior margins of the hind-limbs, that is a kind of tetrapteryx-stage, as suggested by Beebe, even though no relic of this is to be found in the modern squab. But it seems more probable to me that the femora, by the bipedal gait, has been directed so much forward that the

influence of the air on the scales of the hind-limbs was considerably diminished. The reptilian position of the hind-limbs would also have been very unpropitious to the development of a hind-toe.

I am therefore perfectly sure that, even if there possibly may have been such a stage, it was for a comparatively short time only, that it was passed long before the Jurassic birds were developed, and consequently that *Archaeornis* had no pelvic wings. For if it had had any such things, it would have been unable to represent a transitional stage from reptile to bird; the retention of the reptilian position of the hind-limbs would have rendered it a most helpless creature, not adapted to an erect gait, and hence, bound to succumb in its struggle for existence.

Fig. 141 illustrates Beebe's view of the Tetrapteryx and the Archaeopteryx-like stages, as also the reptilian position of the hind-limbs. Strangely enough, he has evidently not thought of lengthening the remiges, which must have taken place throughout the millions and millions of years that passed between the two stages. As a matter of fact, *Archaeornis* had a much larger wing area than shown in Beebe's illustration. My drawing (fig. 141, 3) shows the exact proportions according to the fossil impressions of the wing-feathers, as seen in figs. 20—22. The caudal feathers, too, would no doubt spread out sideways during flight; to all appearance, therefore, a "pelvic wing" was of no use whatever to the bird.

The surprisingly great number of primaries in *Archaeornis* seems to indicate that the wing-feathers in *Proavis* at first were of a large, but not fixed, number, the many scales on the posterior margin of the fore-limbs having developed at the same time. Afterwards the number has then been reduced.

After now having touched on all particulars, as far as possible, in the development of the *Proavis*, thus making it assume a somewhat more tangible form, we are the better prepared for a mental excursion to the remote period when the transformation of the reptile into a bird was in the process of realization, and the bird-class, so to speak, had its first vernal bloom. At that far away time the blood of the small reptile-like creatures, hopping from branch to branch in the trees of the Lower Trias, must have been fermenting with new yearnings and longings. Impelled by an unconscious desire, they tried to jump farther and farther; there was a queer and stimulating sensation of pleasure in straining the efforts to the utmost, almost beyond the bounds of possibility, in challenging the chance of missing, the risk of a dangerous fall; there was an immense discovery in feeling the first supporting effects of the air-current along the tips of their scales.

Then it was that these commenced to lengthen wherever the pressure of air was strongest: on the back margins of the limbs, on the flanks, and along the sides of the tail. And the animal leaping, the fore-limbs spreading more than the hind-limbs, the lobed elongations of the scales grew stronger along the posterior edge of the arms, so that gradually a new shape of parachute was formed, and winged flight came into existence.

The significant progress of this new formation is that the hind-limbs retain



Fig. 142. Restoration of the hypothetic Proavian, by the author.

their free play, and that the animal thus during its arboreal life, in contradistinction to the other parachute-animals, has remained a bipedal. In my opinion, therefore, it is due to the specialization of these very hind-limbs that mainly the fore-limbs and the tail are used for increasing the resistance of air during the gliding fall, and this has proved productive of the new animal form with arm-flight. And it is owing to the weak and more reptile-like hind-limbs of the Pterosaurs that these animals, in spite of the fact that their bodies in several respects assumed a bird-like aspect, turned out to be patagium-flutterers.

We must not think of the entrainment from reptile to bird as taking place along a single line only. Nature is rich and multifarious, and in the different classes of animals we have seen many examples of how, besides the individual stocks surviving to this day, a great number of others arose which became extinct after a shorter or longer lapse of time. This has no doubt also been the case for the small section of animal life with which we here have been dealing. No doubt many futile attempts have been made in attaining the character of the bird, but all of these came only a part of the way; certain defects or weak points have made these stocks succumb in their competition with the one that was best equipped, the only one that finally succeeded in becoming a bird.

Well, then there is no more to be said. We have got to the end of our attempt to account for the origin of birds.

Let us now, in closing, briefly recapitulate the results arrived at.

It is beyond all doubt that the birds are descended from reptiles. The point of departure is probably among the Pseudosuchians. In the course of time, these reptiles with increased frequency raise the forepart of their body from the ground and move about on the hind-limbs only, thus little by little assuming a bipedal gait. In consequence, their hind-limbs become more adapted to this mode of walking, the femur being directed more forward, the foot centering about the median line, the metatarsals becoming elongate and more closely appressed, and the third toe growing the longest, the fifth one at the same time diminishing.

From being a terrestrial runner the animal now turns an arboreal climber, leaping farther and farther, from branch to branch, from tree to tree, and from the trees to the ground. Meanwhile the first toe changes into a hind-toe, so adapted as to grasp the branches. As the hind-limbs, while running on the ground, have abandoned their reptilian position, they are kept closer to the body when leaping takes place, the pressure of air, acting like a stimulus, produces, chiefly on the fore-limbs and the tail, a parachutal plane consisting of longish scales developing along the posterior edge of the forearm and the side-edges of the flattened tail.

By the friction of the air, the outer edges of the scales become frayed, the frayings gradually changing into still longer horny processes, which in course of time become more and more feather-like, until the perfect feather is produced. From wings, tail, and flanks, the feathering spreads to the whole body.

The lengthening of the penultimate phalanges of the fingers is attained by using the claws for climbing, and this elongation has been very propitious to the subsequent development of the wing.

The more intensive use of the arms, however, has also lengthened these, laid claim to more powerful muscles for the movements of same; this again has reacted upon the breast-bone, the two lateral halves of which have coalesced and ossified completely, forming a projecting ridge for the origin of muscles.

The accelerated metabolic process, finally, produced an increased caloricity,

protected by the feathering, until the warm-blooded state was attained. The air-sacs of the lungs have expanded, spreading through the whole body and filling the bones with air. The increase of all these activities, moreover, has also resulted in a considerable enlargement and a somewhat refining evolution of the brain.

In this way the reptile, through millions of years and innumerable generations, has been changed into a bird.

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